THE BRAINCASE, BASICRANIAL AXIS AND MEDIAN SEPTUM IN THE DINOCEPHALIA

By

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(With 58 figures)

Contents

Introduction

During the past few years I have been able to collect some interesting cranial material of three of the infra-orders of the suborder Dinocephalia. Part of this material has been collected with financial aid from the South African Council for Scientific and Industrial Research. To this Council I am moreover indebted for funds which made the acquisition of diamond-studded circular saws for cutting serial sections possible. This method has revealed important points of structure which would have been wellnigh impossible to ascertain at all accurately by the hammer-and-chisel technique on which I have had to rely hitherto.

Material

All previously described specimens have been re-examined and the following new material has been studied:

TAPINOCEPHALIA

S.A.M. 5584 *Struthiocephalus* sp., Abrahamskraal, Prince Albert. Pres. W. van der Byl 1919.

This specimen consists of a partially disarticulated skull. Through the posterior part of the skull a number of longitudinal sections have been cut to show the posterior part of the braincase and the parietal tube in sagittal section.

Ann. S. Afr. Mus. **50** (10), 1968: 195–273, 58 figs.

S.A.M. 9129 *Struthiocephalus* sp., Voëlfontein, Prince Albert. Collected L. D. Boonstra 1929.

This consists of an isolated lower half of an occiput beautifully preserved. It has been cut through sagittally and the left half of the posterior part of the braincase has been exposed internally.

S.A.M. 12294 *Keratocephalus moloch*, Boesmansrivier, Beaufort West. Collected L. D. Boonstra 1937.

This specimen consists of the posterior half of a skull. Both sides of the braincase have been well exposed and a sagittal cut has enabled me to clear the left half of the endocranial cavity.

S.A.M. 11701 *Criocephalus* sp., Elandsberg, Sutherland. Collected L. D. Boonstra 1946.

This specimen consists mainly of an incomplete occiput and skull-cap through which a sagittal cut has been made to show the parietal tube and adjacent bones.

S.A.M. 11972 *Moschops capensis*, Kruisvlei, Beaufort West. Collected L. D. Boonstra 1929.

The specimen consists of a good posterior half of a skull figured in 1957. A block has now been cut out of the middle portion and this has been serially sectioned in the transverse plane to study the internal structure of the braincase and adjacent structures.

S.A.M. 11985 *Moschops* sp., Dikbome, Laingsburg. Collected L. D. Boonstra 1951.

This is a beautifully preserved lower half of an occiput in which the posterior part of the braincase has been exposed internally.

S.A.M. 12046 *Criocephalus* sp., Skoppelmaaikraal, Laingsburg. Collected L. D. Boonstra and H. Zinn 1956.

A skull-cap in which most of the surface bone has been weathered away, but a longitudinal cut has exposed the parietal tube in sagittal section.

S.A.M. 12049 *Struthiocephalus whaitsi*, Dwarsrivier, Laingsburg. Collected L. D. Boonstra and A. Bothma 1957.

This is a good skull, which on exposure has fortuitously cracked through in a more or less longitudinal plane, so that I have been able to clean the whole of the braincase internally and take a direct cast of the endocranial cavity.

S.A.M. 12060 *Mormosaurus* sp., Aasvoëlbos, Beaufort West. Collected L. D. Boonstra and G. S. Victor 1957.

This specimen located by Mr. Victor consists of a very good skull fractured longitudinally, so that I could study the left half in the conventional manner and of the right half I have cut a consecutive series of 76 transverse sections.

S.A.M. 12062 *Struthiocephalus* sp., Skoenmaker, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A skull-cap through which some longitudinal sections have exposed the parietal tube in sagittal section.

S.A.M. 12066 *Criocephalus* sp., Skoenmaker, Beaufort West. Collected L. D. Boonstra 1957.

This is a well preserved skull cap showing much of the outer surface and a sagittal cut has exposed the whole parietal tube.

S.A.M. 12091 *Struthiocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A skull-cap in which a number of transverse sections have shown the nature of the olfactory tracts and the pineal tube.

S.A.M. 12092 *Struthiocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A fair skull in which a series of longitudinal sections have revealed much of the structure of the braincase.

S.A.M. 12093 and 12094 *Keratocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

These two skulls have by natural weathering exposed much of the internal structure of the braincase.

S.A.M. K268. *Criocephalus gunyankaensis*, Gunyankás Kraal, Busi Valley, Southern Rhodesia. Pres. A. M. MacGregor 1945.

Posterior parts of crania showing little of the structure but with most interesting evidence of the parietal organ.

TITANOSUCHIA

S.A.M. 11486 *Jonkeria* sp., Mynhardtskraal, Beaufort West. Collected L. D. Boonstra 1940.

A good snout of which the one half has been serially sectioned transversely to show the structure of the anterior part of the median septum.

S.A.M. 11556 *Jonkeria* sp., Mynhardtskraal, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A skull of which the outer surface has mostly been weathered away. I have cut a block out of the middle part of the back of the skull and this has been serially sectioned in the transverse plane to study the braincase.

S.A.M. 11574 *Jonkeria* sp., Klein-Koedoeskop, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A fairly good skull of which 144 consecutive transverse sections have been cut and from which much of the internal cranial structure can be determined.

S.A.M. 11575 *Jonkeria* sp., Klein-Koedoeskop, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A snout serially sectioned in the transverse plane.

S.A.M. 11884 *Jonkeria vanderbyli*, Skroefpaal, Prince Albert. Collected L. D. Boonstra and P. J. Rossouw 1948.

A good skull in which the braincase has been exposed laterally by conventional preparation.

ANTEOSAURIA

S.A.M. 9085 *Anteosaurus* sp., Boesmansrivier, Beaufort West. Collected L. D. Boonstra 1929.

A snout from which a number of transverse slabs have been cut.

S.A.M. 12082 *Anteosaurus* sp., Boesmanskop, Beaufort West. Collected L. D. Boonstra, H. Zinn and A. Viviers 1957.

An imperfect skull contained in blocks of sandstone. Serial transverse sections have revealed some interesting internal structures.

ANOMODONTIA

S.A.M. 12217 *Dicynodon* sp., Buffelsvlei, Beaufort West, Collected L. D. Boonstra and J. Marais 1959.

Serially sectioned.

THEROCEPHALIA

S.A.M. K210 *Maraisaurus parvus*, Lammerkraal, Prince Albert. Collected L. D. Boonstra 1959.

Serially sectioned.

S.A.M. K253 *Pristerognathoides* sp., Rietfontein, Prince Albert. Collected L. D. Boonstra 1960.

Serially sectioned.

Technique

A number of specimens have been prepared conventionally by mechanical means to expose the surface features of the cranial base from the ventral side and the braincase and interorbital, septum and anterior dermal septum in lateral view using hammer and chisel, vibro-needles and abrasive burrs.

In a few cases fortuitous natural fractures have enabled me to expose the internal faces of the endocranial cavity mechanically. In some others I have cut posterior parts of skulls longitudinally and was thus enabled to remove the infilling matrix in the endocranial cavity mechanically.

Certain pieces of the posterior parts of fragmentary skulls were cut by circular diamond-studded saws into slabs longitudinally. If luckily cut in the right plane quick results were obtained especially for sections in the sagittal plane. But in general longitudinal serial sectioning is unsatisfactory.

The best results were obtained when cutting thin slabs serially in a transverse plane. Although the thickness of the blade caused some loss, the fact that neither the skulls themselves were symmetrical nor the cut truly transverse usually resulted in a loss on one side only. I first used a large diameter saw to cut through the whole skull, but later got better results by first cutting a rectangular block out of the middle of the skull and then serially sectioning the smaller block with a smaller and thinner blade.

The sections were lightly etched with hydrochloric acid, which also caused a differential bleaching action in many cases.

By making sure that one always has a base line, it is easy to obtain graphical reconstructions in planes at right angles to the sections.

Although I have not done so it will be quite easy to prepare reconstructions in three dimensions in wax or any other suitable material.

In those cases where the endocranial cavity was cleaned mechanically I have made casts in a pliable material (Minimould and Revultex).

I may add here that when contemplating cutting serial sections with a diamond-studded circular saw only suitable material should be selected. In any case, only saws which polish as well as cut should be used.

Sound skulls, unweathered and with little fracturing or cracks, should be selected.

Specimens in an arenaceous matrix are better than those in a more argillaceous matrix because in the latter the differentiation between bone and matrix is difficult to obtain by the etching process I have used.

Descriptions of the specimens systematically

TAPINOCEPHALIA

S.A.M. 5584 *Struthiocephalus* sp. (Fig. 1)

A number of longitudinal sections have been cut through the posterior third of a skull and the posterior part of the braincase and the parietal tube is

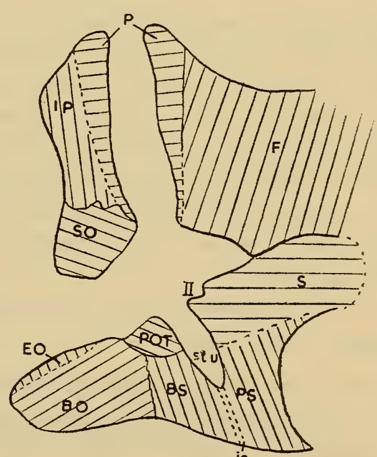


Fig. 1. *Struthiocephalus* sp. S.A.M. 5584 × ¼. Sagittal section of the posterior part of the skull.

See overleaf for key to this and the other figures in this paper

KEY TO THE FIGURES

abnp — anterior border of the nasal passage
ac — accessory carotid foramen
bol — olfactory bulb
BS — basisphenoid
bpp — basipterygoid process
C — canine
ch — choana
ds — dorsum sellae
E.O. — exocipital
E.P. — epipterygoid
F — frontal
fj — jugular foramen
fl — flocculus
fo — fenestra ovalis
fob — foramen for opthalmic branches of V and VII
FS — frontosphenoid
fvc — foramen entering vomerine canal for the branch of the naso-palatine nerve
hy — hypophysis
iam — internal auditory meatus
ic — internal carotid foramen
I.P. — interparietal (postparietal, dermo-supraoccipital)
ipv — interpterygoid vacuity
L — lacrimal
lob — lobus olfactorius
lrp — lateral ramus of the pterygoid
mcv — medial cerebral vein
med — medulla
N — nasal
nob — notch for the opthalmic branch of V and VII
np — notochordal pit in the basioccipital
obg — groove for the olfactory bulb
OO — opisthotic
OS — orbitosphenoid
P — parietal
PA — palatine
PBS — parabasisphenoid
pc — postcanine
pin — pineal (parietal) foramen or tube
PM — premaxilla
POC — paroccipital
PO — postorbital
PF — postfrontal
PP — postparietal
PRF — prefrontal
POT — proötic
PRS — presphenoid
PS — parasphenoid
PT — pterygoid
ptf — posttemporal fossa
pts — septum of the pterygoid
qr — quadrate ramus of the pterygoid
S — sphenoid-complex
seo — sutural face for the exoccipital
sep — sutural face for the epipterygoid
sip — sutural face for the interparietal
sp — sutural face for the parietal
spbs — sutural face for the parabasisphenoid
spt — sutural face for the pterygoid
sq — sutural face for the quadrate
ssq — sutural face for the squamosal
st — sutural face for the tabular
SM — septomaxilla
smf — septomaxillary foramen
sml — ledge of septomaxillary
sms — spur of septomaxilla
SO — supraoccipital
SS — septosphenoid
ST — stapes
stu — sella turcica
tol — tractus olfactorius
uz — unossified zone
V — vomer
VC — vomer canal for naso-palatine nerve
VS — median septum of the vomer

here figured in sagittal section. Noteworthy features ascertained are: the proötics meet in the median line to form the upper part of the dorsum sellae; the lower half of the sella turcica lies in the basisphenoid and the internal carotids enter at the bottom of the sella; the frontals form part of the roof of the braincase above the olfactory lobes. This specimen also shows that the ascending process of the proötic meets a descending process of the supraoccipital in the lateral wall of the braincase so that the proötic incisure is closed anteriorly to form a large trigeminal fenestra. The parasphenoid and the sphenoidal complex form a median septum.

The constituent parts of the sphenoidal complex are not recognizable as separate ossifications.

S.A.M. 9129 *Struthiocephalus* sp. (Figs 2–4)

This beautifully preserved disarticulated piece of the occiput found as an isolated piece shows a number of features very clearly. In occipital view (fig. 2)

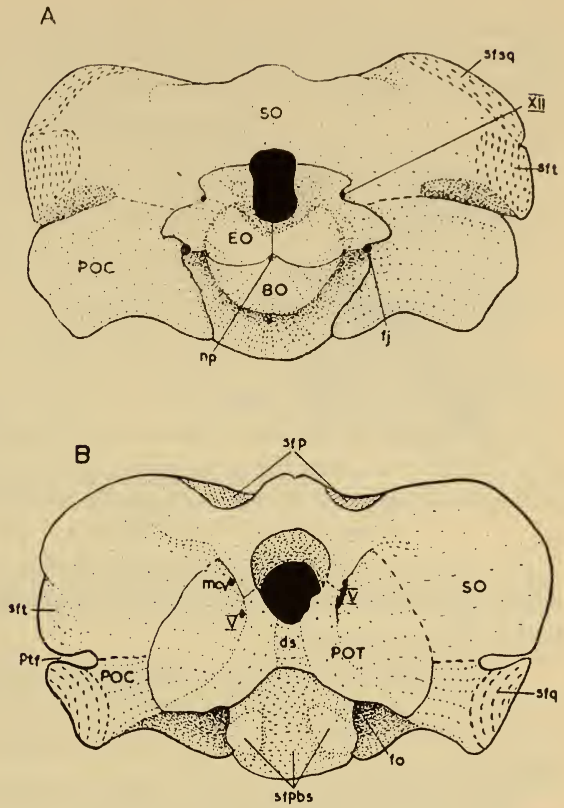


FIG. 2. *Struthiocephalus* sp. S.A.M. 9129 × ½.
A. Posterior view of an isolated occiput. B. Anterior view of an isolated occiput.

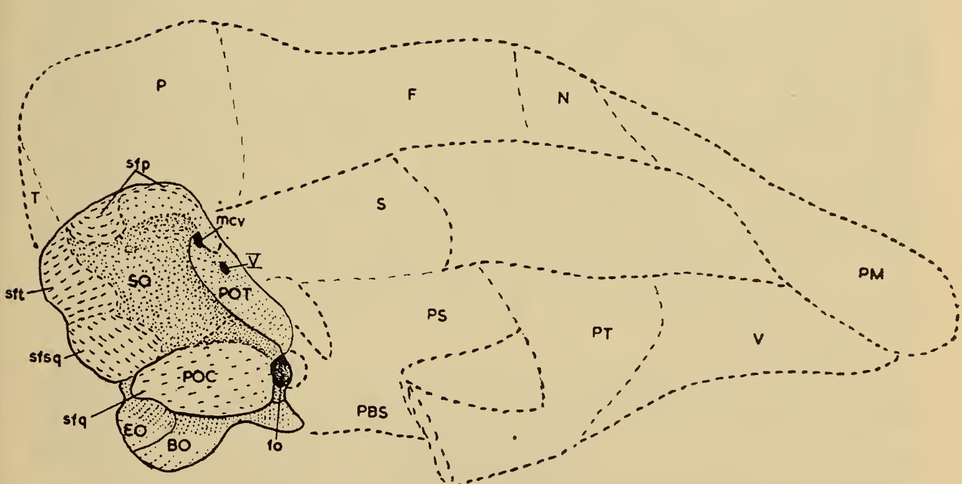


FIG. 3. *Struthiocephalus* sp. S.A.M. 9129 × ½.
Parasagittal view of occipital segment in relation to the rest of the skull (shown in broken lines).

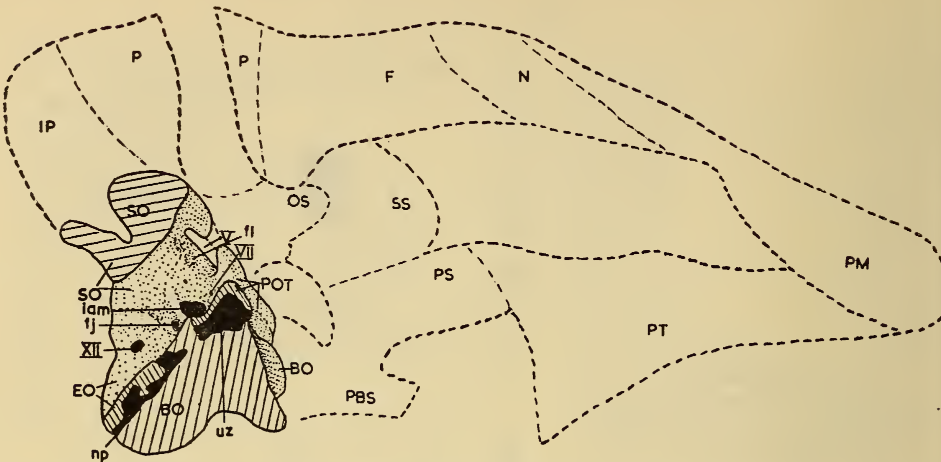


FIG. 4. *Struthiocephalus* sp. S.A.M. 9129 × ¼.
Sagittal view of the occiput cut through in this plane in relation to the rest of the skull shown in broken lines.

the exoccipitals are seen as well-developed bones forming the upper and dorsolateral part of the condyle, the lower and most of the lateral rim of the pinched-in oval foramen magnum.

The hypoglossal foramen is separate from the jugular foramen; the latter is bounded by the basioccipital, exoccipital and opisthotic. The supraoccipital and opisthotic are fused except laterally where they are separated by the slit-like posttemporal fenestra.

The anterior aspect of the occiput is interesting (fig. 2B). The parabasisphenoid is not preserved, having become disarticulated at the suture with the basioccipital to leave the sutural face perfectly preserved. Two rounded knobs of basioccipital fit into depressions in the basisphenoid medial to the fenestra ovalis. The rim of the fenestra ovalis is formed by basioccipital, basisphenoid, opisthotic and proötic. The proötic is clearly shown to be ankylosed to the anterior faces of the supraoccipital and opisthotic. The proötics have a median anterior face forming the upper part of the dorsum sellae. Laterally a process of the proötic ascends to meet a descending process of the supraoccipital to form a pillar, which closes the proötic incisure anteriorly. On the left side there is a large trigeminal fenestra but on the right there are two separate foramina—the upper for the median cerebral vein and the lower for the trigeminalis.

In figure 3 the occiput is shown in lateral view. The extremity of the paroccipital process shows the sutural face with which it abuts against the quadrate. The greatest part of the outer lateral surface of the posterior part of the braincase is seen to be formed by the supraoccipital. Its lateral ends bear sutural faces for the squamosal and the tabular and its dorsal edge sutural faces for the parietal and interparietal. The proötic shows a small lateral face with a closed proötic incisure divided into two separate foramina of which the lower one is for the Vth nerve and the upper for the median cerebral vein. The foramen for the VIIth nerve has not been located with certainty but may emerge lateral to the dorsum sellae through the ascending proötic pillar.

In figure 4 the occiput is shown cut through sagittally and with the inner face of the braincase exposed by mechanical removal of the infilling matrix.

The rounded boss on the anterior sutural face of the basioccipital fitting into the basisphenoid is clearly shown.

Dorsally the basioccipital is separated from both the exoccipital and the proötic in the median line by an unossified zone. Between the exoccipital and the proötic a hump of the basioccipital enters the floor of the braincase.

The hypoglossal nerve leaves the braincase by a large foramen passing through the exoccipital well above the level of the medullary floor. But both the jugular foramen and the internal auditory meatus leave the braincase through openings situated at floor level and both passages are directed downwards and outwards. A sharp ridge separates these two openings. The jugular foramen itself is of moderate size but lies in a deep recess in the sidewall.

The vestibule has a large opening through the sidewall.

A shallow depression in the inner face of the proötic dorso-anteriorly of the vestibule is for the flocculus.

The foramen for the facialis lies anterior to the vestibule and enters the proötic pillar lateral to the dorsum sellae.

S.A.M. 12049 *Struthiocephalus whaitsi* (Figs 5–8)

The outer surface of the braincase (fig. 5) has been prepared by hammer and chisel. Lateral to the braincase proper the supraoccipital and the paroccipital process are seen in section. The posterior part of the sidewall of the braincase is seen to be formed by the supraoccipital, exoccipital and opisthotic. No foramen for the hypoglossal opens externally and there is evidence pointing to its confluence with the jugular tube. The jugular foramen opens at the point where the ex-, basi- and paroccipital meets. The jugular passage has been cleared and is seen to form a long roomy tube 25 mm in length with diameters 4×6 mm.

Dorsally the supraoccipital sends a flange anteriorly to form the middle dorsal part of the sidewall. A process descends anteriorly to the trigeminal fenestra and this meets the ascending process from the proötic. Anteriorly the supraoccipital flange meets the posterior edge of the orbitosphenoid.

The proötic is ankylosed to the anterior face of the opisthotic and has in lateral view a small outer face. An ascending process meets the supraoccipital to enclose a dumbbell-shaped trigeminal fenestra. Ventrally it rests on the ascending part of the basisphenoid to form the anterolateral edge of the dorsum sellae. No external opening for the facialis has been seen.

The opisthotic sends a process towards the fenestra ovalis of which it forms the posterior edge. The rest of the rim is formed by the basisphenoid.

The sphenoid complex rests with its ventral edge on the median septum

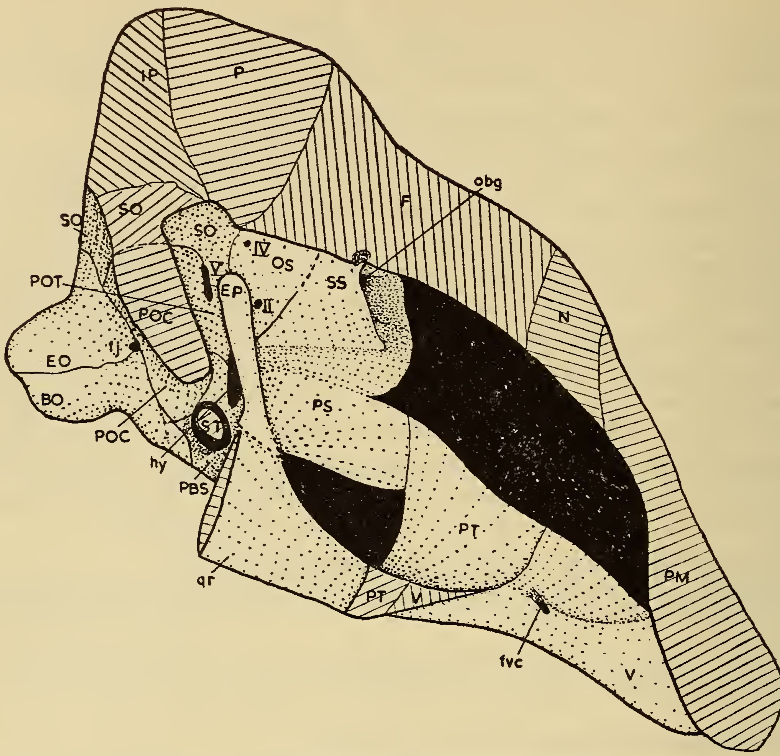


FIG. 5. *Struthiocephalus whaitsi* S.A.M. 12049 × ¼.
Parasagittal view of the skull. Drawn directly from the exposed surface of the internal bones. The occiput, roof-bones and quadrate and lateral ramus of the pterygoid seen in section.

formed by the parasphenoidal rostrum. A step is formed at this contact and a little higher up there is another step running nearly parallel. This recessed strip of bone may represent a distinct ossification—a presphenoid?—and it continues the median septum ventrally composed of the parasphenoid. Higher up the sphenoid complex begins an outward convexity but this still forms part of the median septum. Still further up the convexity curves round the olfactory tract. Anteriorly this outward bulge forms a sharp edge which dorsally bounds the opening from which the olfactory tract emerges and ventrally forms the limit of the recess in which the posterior part of the olfactory bulb is housed. Here a median septum separates the two olfactory bulbs.

In the posterior half of the sphenoid complex there appears to be a suture. Posterior to this suture the sphenoidal complex is pierced by two foramina. The lower one I believe to be for the optic nerve (II) and the upper one for the trochlearis (IV). This part of the complex I have labelled as the orbitosphenoid and the rest is a septosphenoid.

Above the opening from which the olfactory tract emerges there is a small recess in the frontal bone which may have housed an accessory olfactory bulb.

The parasphenoid is fused to the basisphenoid, but the lower part of the sella turcica apparently lies in the basisphenoid, which also appears to form the anterior and dorsal rim of the fenestra ovalis. The anterior rim of the sella appears to be formed by the parasphenoid but as remarked above the ossification here may represent a separate presphenoid. The parasphenoidal rostrum forms a strong but not greatly thickened mèdian septum, which is anteriorly clasped by the ascending septum formed by the pair of pterygoids.

The epipterygoid

Lateral to the braincase and covering much of the open lateral sella lies the epipterygoid. The footplate of the epipterygoid rests on the quadrate ramus of the pterygoid and appears to enter the now immovable basipterygoid joint. The epiterygoid extends obliquely dorsally as a pillar of bone flattened from side to side with fairly straight anterior and posterior edges. Dorsally it has a free rounded edge which does not reach the parietal.

The pterygoid and vomer

Of the palatal complex only the pterygoid and vomer need to be considered here. The pterygoids develop a high and strong septum lying in the median line. Posteriorly they clasp the anterior extremity of the median septum formed by the parasphenoid. Anteriorly the pterygoids are in turn clasped by the well-developed median septal sheets developed by the vomers. On the lateral surface of the vomer at the transition between the vomerine interchoanal bar and the vomerine septum there is a foramen entering the vomer from behind and traversing the bone in anterior direction as a roomy canal or tube, which probably housed the naso-palatine nerve.

The inner surface of the braincase (Fig. 6)

A fortuitous natural longitudinal fracture through the skull has enabled me to clear the endocranium of the infilling matrix. This was accomplished by a laborious process of grinding with corrundum burrs. If used with care a good surface can be obtained with a grinding tool, notwithstanding the contrary opinion expressed by a well-known colleague. When nearing the surface of the bone a flicking action with the burr causes the remaining film of matrix to flick cleanly away leaving an unground face less marked than when a metal point is used as a chisel even in the form of a vibro-needle.

Posterior to the plane of the dorsum sellae the floor of the braincase is formed by the proötics, basioccipital and exoccipital and the sidewall by the exoccipital, supraoccipital, opisthotic and the proötic. The hypoglossal nerve leaves through a small foramen through the exoccipital just above the floor level. The foramen jugulare is large and bounded by the opisthotic, and exoccipital and lies at floor level. Its canal is directed latero-ventrally. The vestibule is widely open and extends to below floor level. The opening is bounded by the opisthotic, basioccipital and proötic. Anterior to the vestibule lies the transverse ridge formed by the proötics whose anterior faces form the upper part of the

FIG. 6. *Struthiocephalus whaitsi* S.A.M. 12049 × ¼.
Sagittal view of the skull. Drawn partly from a fractured face and the exposed endocranial cavity, but otherwise reconstructed.

dorsum sellae which is pierced by a foramen for the VIth cranial nerve. Dorsally the sidewall is pierced by a large dumbbell-shaped trigeminal fenestra whose opening is directed much anteriorly. It is anteriorly bounded by processes of the proötic and the supraoccipital.

Anteriorly the posterior flange of the sphenoidal complex meets the supraoccipital and proötic above the sella turcica. This sheet of bone is pierced by three foramina, the upper one near the suture with the parietal is for the IVth nerve; the middle one, just anterior to the proötic suture, is for the IIIrd nerve; the third, situated on the floor is for the exit of the optic nerve. This part of the complex represents an orbitosphenoid.

Anteriorly as well as ventrally the sphenoid complex forms a median septum. The posterior part is the presphenoid. The anterior part which separates the olfactory tracts and rests on the parasphenoid may be called a septosphenoid.

The parietal canal is wholly enclosed by the parietals. In median section it is a roomy tube with a posterior bulge in its lower part. Its length is 105 mm and in its upper part the diameters are 25 × 25 mm. Where it enters the braincase proper it is constricted.

The endocranial cast (Fig. 7)

From the cleaned endocranial cavity I have made an endocranial cast using a pliable rubber compound (revultex). Of this cast I am including here outline drawings as projected from the side and from above.

It is obvious that such a cast is of the endocranial cavity and not of the brain, which did not fill the cavity, with the result that the various divisions of the brain are but vaguely indicated.

Of the forebrain (prosencephalon) the shape of the olfactory bulbs cannot be determined as they were for the greater part not enclosed in bone. The olfactory tracts, lying as they do in tubes formed by the septosphenoid, can be distinguished. The tract was short and oval in cross-section. The olfactory lobe is indicated by a small laterally directed bulge. The position of the thalamus is indicated by the position of the optic stalk and the pituitary cavity. The hypophysial or pituitary cavity is enormous. How much of the cavity was filled by infundibulum, pituitary and accessory structures cannot be determined, but the tendency to gigantism and the pachyostosis would indicate the presence of a large pituitary gland.

Above the thalamus lies the truly enormous parietal canal or tube. If the soft structures completely fill this space their mass would be considerable. The volume in this specimen is ± 65 cc and the total volume of the endocranial cast (with allowance made for the olfactory bulbs) is ± 270 cc.

In vertebrates a number of structures are known arising from the brain

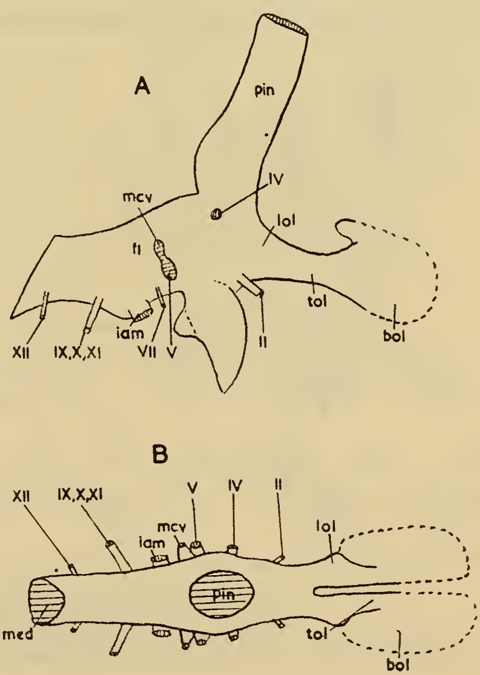


Fig. 7. *Struthiocephalus whaitsi* S.A.M. 12049 × ¼. A plastic cast taken from the cleaned endocranial cavity drawn in: A. Lateral view. B. Dorsal view with the root of the pineal mass seen in section.

near the junction of the fore- and mid-brain. From fossil material it is impossible to say which of these structures—epiphysis, paraphysis, pineal organ or parietal organ—were present in life or what part of the parietal canal was occupied by each component part of what we have to call the 'parietal' organ.

The large volume of the parietal organ in the Dinocephalia is unique. Part of the material may have been glandular as is the pineal gland of mammals which secretes internally.

Part of the mass was certainly nervous with a receptor function either visual or thermal or both. By analogy with living forms a thermo-regulatory function is probable.

The optic lobe of the midbrain would lie posterior to the emergence of the IInd nerve.

The flocculus can be determined as a slight bulge just posterior to the trigeminal fenestra and above the vestibule.

The IXth, Xth, and XIth nerves leave the medulla low down, but the XIIth emerges somewhat higher up from the lateral face of the medulla.

The basicranial axis (Fig. 8)

In figure 8A the bones of the basicranial axis are shown in relation to the occipital and the otic bones and the pterygoid of the palatoquadrate as exposed in ventral view. It is thus evident that the parasphenoidal rostrum is directed obliquely upwards so that the pterygoids meet below it, but its tip can be seen through the interpterygoid vacuity. The pterygoid has a long suture with the parabasisphenoid reducing the original joint between the palatoquadrate and

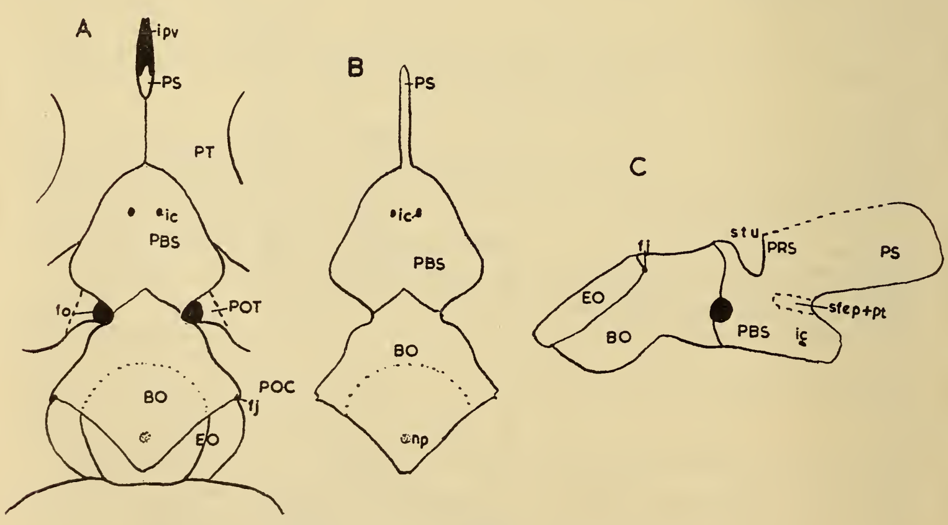


FIG. 8. *Struthiocephalus whaitsi* S.A.M. 12049 × ¼.
The basicranial axis as reconstructed. A. Ventral view in relation to supporting bones. B. Ventral view. C. Lateral view.

the braincase to immobility.

In figure 8B the basioccipital-parabasisphenoidal complex is shown disarticulated. In figure 8C the disarticulated complex is shown in lateral view. Points of interest are: the large sella turcica is a pit in the basisphenoid, with the anterior face probably formed by the presphenoid; the parasphenoidal rostrum forms a septum directed antero-dorsally; thè original basipterygoid process is indicated in broken lines forming an immovable sutural face for both the epipterygoid and the pterygoid.

The position of the fenestra ovalis is shown in black. This fenestra leads into the opisthotic in which the inner ear lies.

S.A.M. 12062 *Struthiocephalus* sp. (Fig. 9)

From a number of longitudinal sections cut through the posterior part of a poor skull I have reconstructed a section in a plane just lateral of the median plane to show, in particular, the olfactory tract in longitudinal section and the canal for the internal carotid. An unossified zone is present in the anterior part of the basioccipital.

The parietal tube is 97 mm in length with average diameters 23 × 26 mm.

S.A.M. 12091 *Struthiocephalus* sp. (Fig. 10)

Cross-sections of the olfactory and pineal regions

1. The anterior end of the sphenoidal complex consisting of a septosphenoid is seen to be wedged in between the frontals. Laterally there is a deep groove in the under surface of the frontal which apparently housed a large olfactory bulb.
2. A sharp wedge of the septosphenoid is dorsally intercalated between the frontals. Laterally the septosphenoid develops a lateral flange forming a groove to hold the olfactory bulb.
3. Further back the wings composed of the orbitosphenoids enclose the olfactory tracts which are dumbbell-shaped in cross-section.

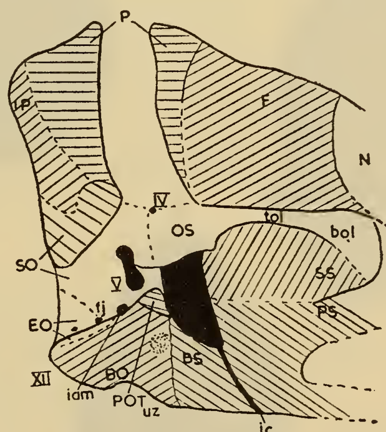


Fig. 9. *Struthiocephalus* sp. S.A.M. 12062 × ¼. A longitudinal section of the posterior part of the skull just lateral to the median line.

4. Still further back the upper part of the median septum is lost and the two separate olfactory tracts fuse and house the unpaired olfactory lobes.
5. This section shows the parietal tube in cross-section in the plane of the emergence of the IVth cranial nerve. Note the irregular outline of the tube.
6. Further back the parietal canal presents an elongated pear-shaped out-

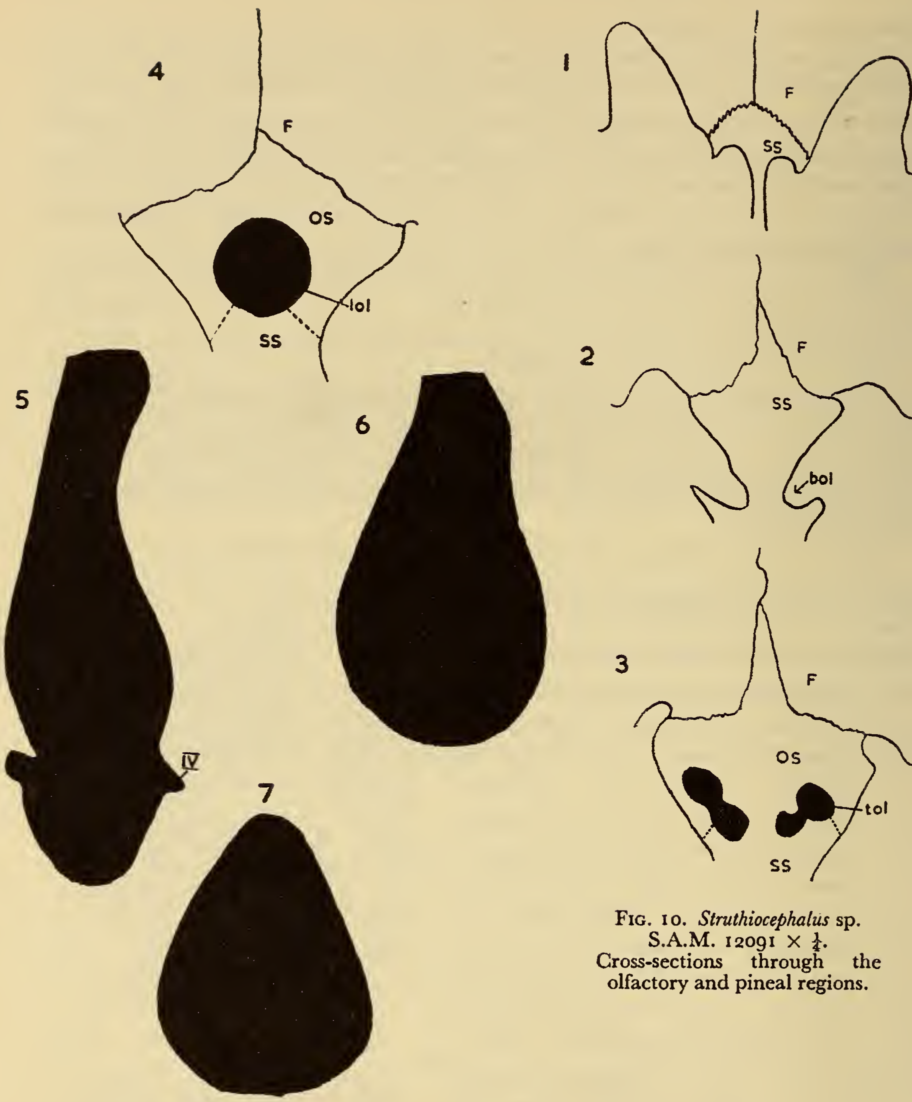


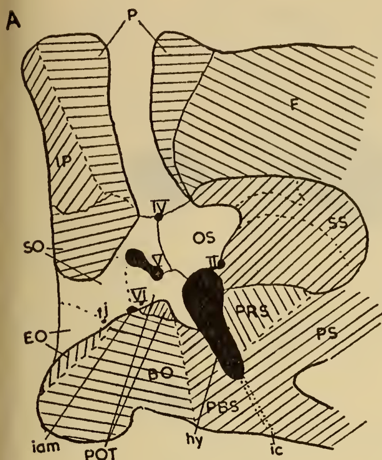
Fig. 10. *Struthiocephalus* sp. S.A.M. 12091 × ¼. Cross-sections through the olfactory and pineal regions.

line in cross-section.

7. And a cross-section through the posterior bulge of the parietal tube presents a squat pear-shaped outline.

S.A.M. 12092 *Struthiocephalus* sp. (Fig. 11)

From a longitudinal fracture and a number of longitudinal sections I have been able to reconstruct and figure the braincase in sagittal section and in lateral view. The structural relations determined corroborates the findings arrived at from other specimens of *Struthiocephalus*. In addition this specimen shows that anterior to the sella turcica the bone fibres in the parasphenoidal part of the median septum diverge and this I take to indicate that the lower



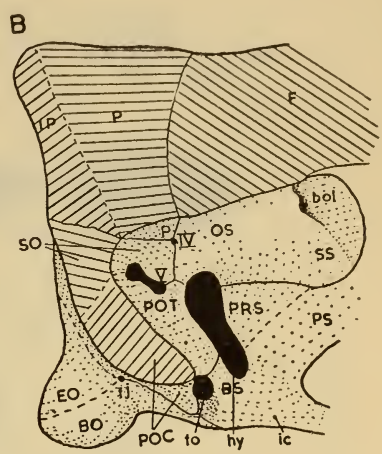


FIG. 11. *Struthiocephalus* sp. S.A.M. 12092 × ¼. Two reconstructed views of the posterior part of the skull. A. Sagittal view. B. Parasagittal view.

part is composed of the parasphenoid, and that the upper part, forming most of the anterior border of the sella turcica, may represent a distinct presphenoid.

S.A.M. 12060 *Mormosaurus* sp. (Figs 12–16)

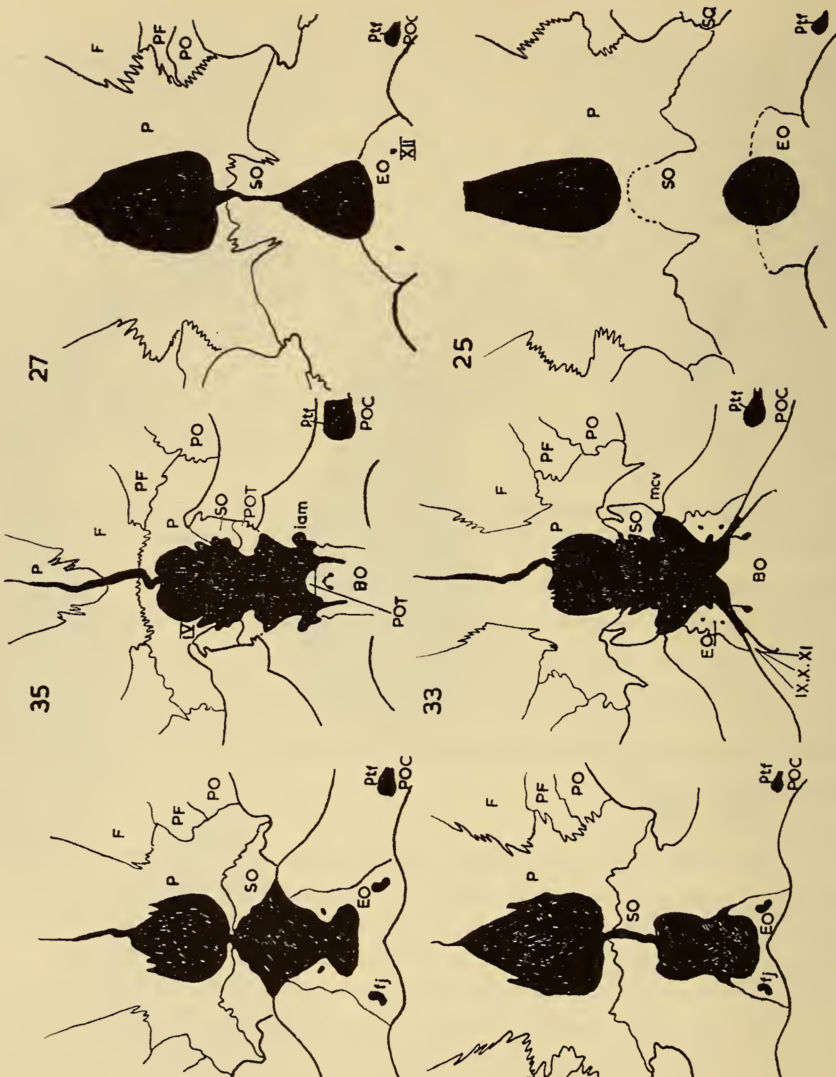
This specimen consists of a good skull of which the snout has been weathered away. A longitudinal fracture has made it possible to study the left half of the skull conventionally and to make a series of cross-sections of the posterior part of the right half of the skull. I have combined the results so obtained to produce reconstructed figures showing the skull in sagittal and in parasagittal view.

A series of cross-sections (Fig. 12)

To show the nature of the endocranial cavity and the structure of the bony braincase I am reproducing here a series of cross-sections. This series of sixteen sections consists of the consecutive odd numbers, commencing anteriorly in the plane of the olfactory bulbs. The sections are at intervals of 9 mm.

55. This section passes through the anterior end of the sphenoidal complex and shows this complex forming a median septum with its upper end intercalated between the two frontals and its lower end resting on the rostral part of the parasphenoid. In the upper part of its lateral face the recess for housing the olfactory bulb is well developed. Below this recess the bone forms a stout septum whose inner part consists of cancellous bone, lateral of which is an unossified zone which in turn is flanked by a strip of compact bone. The septum then abruptly narrows and rests on the fairly thin upper edge of the parasphenoid. The section passes through the parabasisphenoid just posterior to the original basipterygoidal joint.

The pair of foramina for the internal carotids are seen in their passage through the bone. The parasphenoid is completely fused with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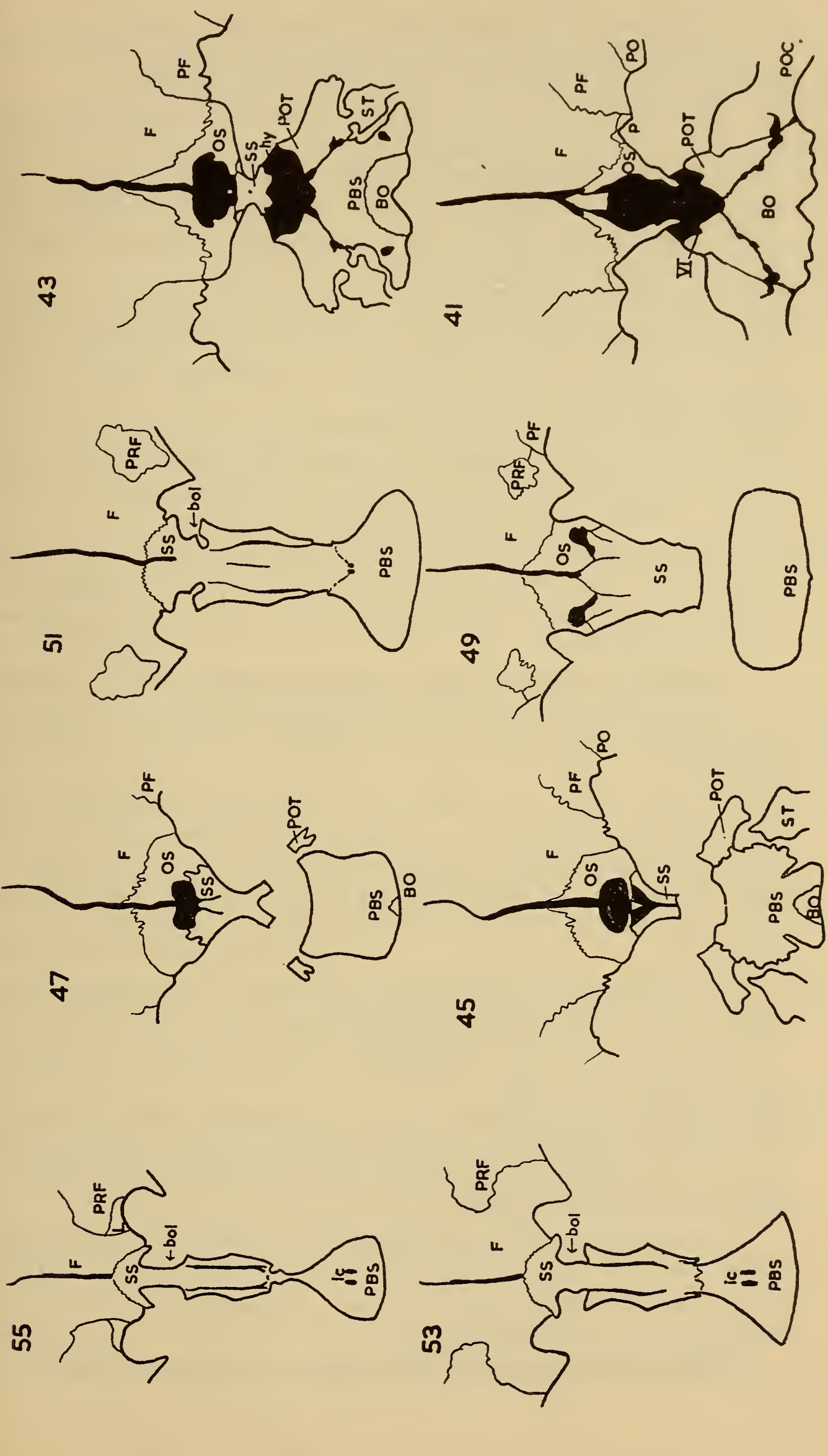


FIG. 12. *Mormosaurus* sp. S.A.M. 12060 × $\frac{1}{4}$.
A consecutive series of cross-sections through the braincase from back to front.

the basisphenoid with no indication of their relative contribution.

Lateral to the recess in the septosphenoid the under surface of the roof-bones is also excavated to house the olfactory bulb.

53. The olfactory recess in the septosphenoid is deeper, the septosphenoidal part of the septum is thickened as is also the parasphenoidal part on which it rests. The lateral compact face of the septosphenoid is still separated from the internal cancellous part by a strip of matrix. It would appear that this separation is a postmortem feature and that it does not indicate the presence of two separate bones.

51. The olfactory recess develops a deeper pocket which is nearly closed off laterally. The septum becomes greatly thickened and rests on the wide upper edge of the stout parasphenoid. In the upper part there is a wide median suture in the septosphenoid.

49. The olfactory tracts are enclosed in tubes formed by the orbitosphenoid. The septosphenoid no longer rests on the parasphenoid, because of the presence of the sella turcica developed in the parabasisphenoid. Dorsally there is a median suture which bifurcates ventrally.

47. The pair of separate tubes for the olfactory tracts have in this plane coalesced to form a single kidney-shaped tube which now houses the olfactory lobes. Ventrally the septosphenoid is forked to form a domed roof to the sella turcica.

Laterally the anterior edge of the proötic begins to form a lateral wall to the sella turcica in its lower part. Above the olfactory lobes there is a persistent open median suture, and below the brain this suture bifurcates.

45. The forebrain is housed in a single tube bounded by the orbitosphenoids. Below the forebrain a median suture in the ventral part of the septum bifurcates dorsally to form a pair of widely open spaces. Lateral to these fissures there is a suture separating the upper orbitosphenoidal part from the lower paired septum. This septal part is formed by a septosphenoid.

Ventrally the parabasisphenoid still forms the floor and part of the dorsum sellae. The proötic is extending dorsally into the sidewall.

The proötic and parabasisphenoid are seen to form an irregular rim of the fenestra ovalis.

43. The forebrain is still enclosed in the orbitosphenoid, which is dorsally deeply intercalated between the frontals in the median plane, except for the floor which is now formed by the septosphenoid. The median septum is now low but broad.

A spur of the proötic is seen to extend well dorsally and is extending medially to enter the dorsum sellae which is, however, still mainly formed by the basisphenoid. The proötic is separated from the parabasisphenoid by an unossified zone.

Within the fenestra ovalis the proötic is connected to the stapes by a neck of bone, with no indication of any suture in between.

41. The median septum below the brain ends in this plane. The ventral edge of the orbitosphenoid nearly meets the ascending proötic to close up the sidewall.

    The proötics nearly meet in the middle line, where the basioccipital still forms the middle part of the dorsum sellae. A notch in the proötic is for the VIth nerve.

39. The orbitosphenoid has met the ascending proötic to close off the sidewall of the braincase which has been open laterally of the sella turcica.

    The proötics meet in the median line to form the upper part of the dorsum sellae. The foramen for the VIth nerve passes through the proötic part of the dorsum sellae.

37. In this plane the anterior end of the supraoccipital flange has taken over the formation of the sidewall of the braincase from the orbitosphenoid.

    The anterior border of the parietal canal is formed by the parietals and the floor of the braincase by the proötics. Note the unossified zone between the proötics and the basioccipital.

    There is an opening in the sidewall through the proötic for the Vth nerve.

35. The sidewall is here formed by the supraoccipital, proötic and the opisthotic.

    The vestibule lies in the opisthotic and basioccipital.

33. An opening laterally between the supraoccipital and the opisthotic is for the exit of the middle cerebral vein. Just posterior to the vestibule there is a foramen low down at floor level for the exit of the IXth, Xth, and XIth nerves.

31. Here the exoccipital forms the floor on which the medulla rests.

29. The medulla is encased in the supraoccipital and the exoccipital.

27 & 25. Shows sections through the parietal canal and the medulla.

Lateral view of the braincase (Fig. 13)

Laterally the brain is seen to be enclosed in bone, except for the absence of a lateral wall to the sella turcica and the olfactory bulbs.

The anterior part of the braincase is formed by the sphenoid complex composed of orbito- and septosphenoid.

The posterior part is enclosed by the bones of the otic capsule—proötic and opisthotic—and the occipital bones—supraoccipital and exoccipital.

The sphenoidal septum rests on the parasphenoid.

The anterior median septum is formed by septal upgrowths of the pterygoid flanked by sheets from the vomers.

The pterygoidal septum clasps the anterior end of the parasphenoidal septum.

Epipterygoid

The epipterygoid has a short footplate without posterior process, standing

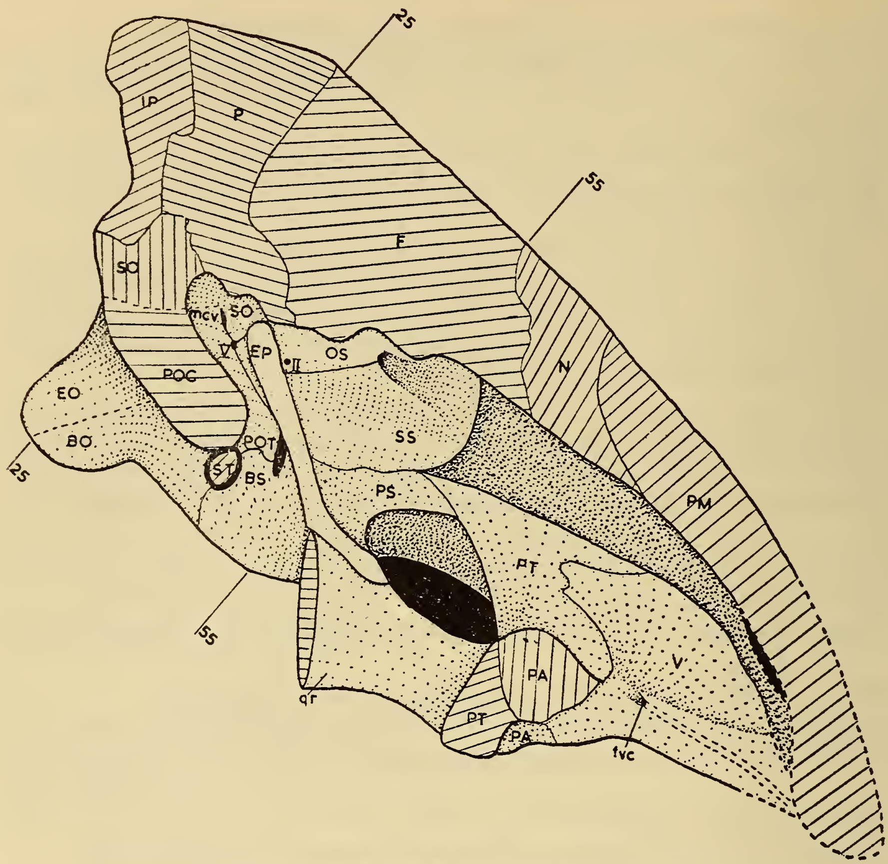


Fig. 13. *Mormosaurus* sp. S.A.M. 12060 × ½.
A parasagittal view of the skull drawn partly from cross-sections and partly directly from a fracture surface 25—25, 55–55 indicates location of cross-sections.

on the quadrate ramus of the pterygoid. From here it rises obliquely in the skull as a fairly slender rod to reach the anterior lateral flange of the supraoccipital just below the ventral surface of the parietal.

Sagittal view (Fig. 14)

In sagittal section it is seen that the floor of the braincase is formed by the exoccipitals, basioccipital, proötics, basisphenoid, orbito- and septosphenoids.

The inner lateral face of the endocranial cavity is formed by the exoccipital, supraoccipital, opisthotic, proötic and orbitosphenoid.

The vestibule, and the foramina for the vagus complex and the XIIth nerve lie low down at floor level.

The trigeminal fenestra lies half-way up and is bounded by the supraoccipital and proötic.

The optic nerve leaves the endocranium low down through the

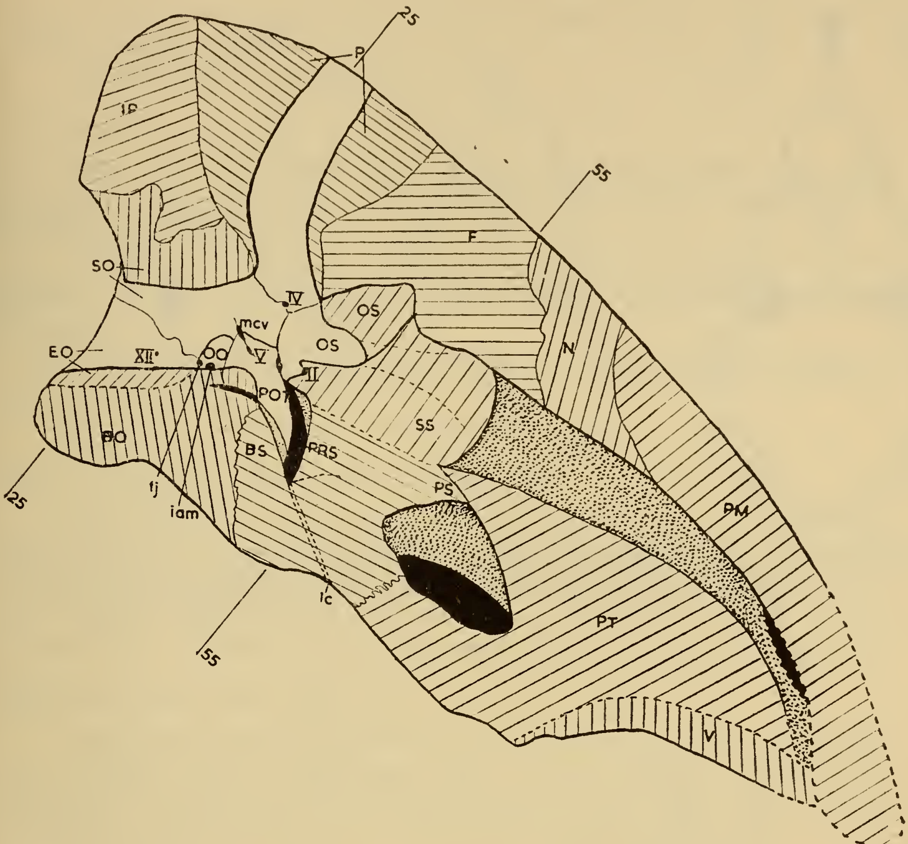


FIG. 14. *Mormosaurus* sp. S.A.M. 12060 × ¼.
A sagittal view of the skull reconstructed from a series of cross-sections and a longitudinal fracture.

orbitosphenoid.

The IVth nerve has its foramen bounded by the supraoccipital and the parietal high up in the sidewall.

The median part of the anterior septum is seen to be formed by the pterygoid with the septosphenoid and parasphenoid and presphenoid forming the interorbital part of the septum.

The basicranium (Fig. 15)

In ventral view it can be clearly seen that the basicranium has a long sutural contact with the pterygoid and epiterygoid, with no movement between these two segments.

A lateral process of the parabasisphenoid bounds the fenestra ovalis anteriorly and a similar process of the basioccipital bounds it postero-ventrally,

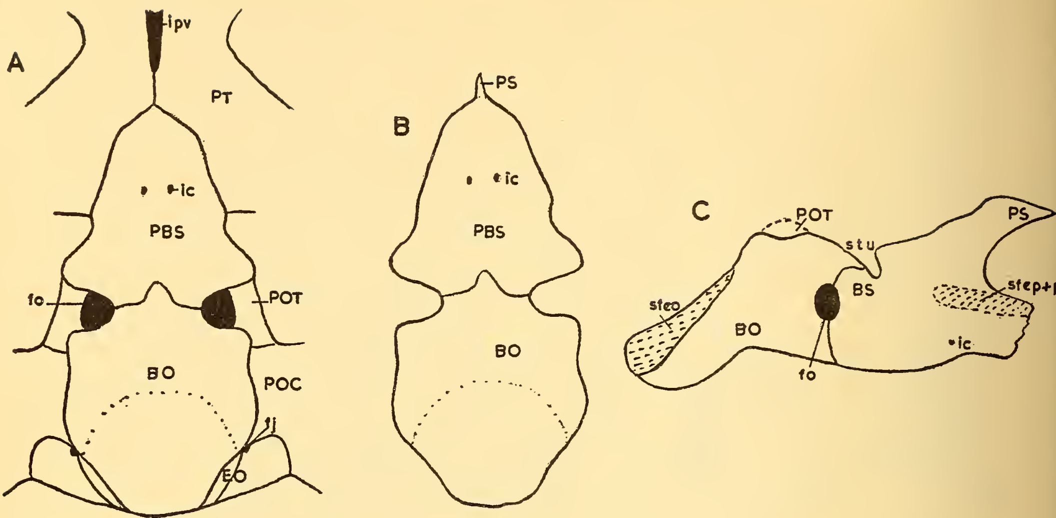


Fig. 15. *Mormosaurus* sp. S.A.M. 12060 × ¼.
The basicranial axis reconstructed from cross-sections and direct observation. A. Ventral view in relation to the supporting bones. B. Ventral view. C. Lateral view.

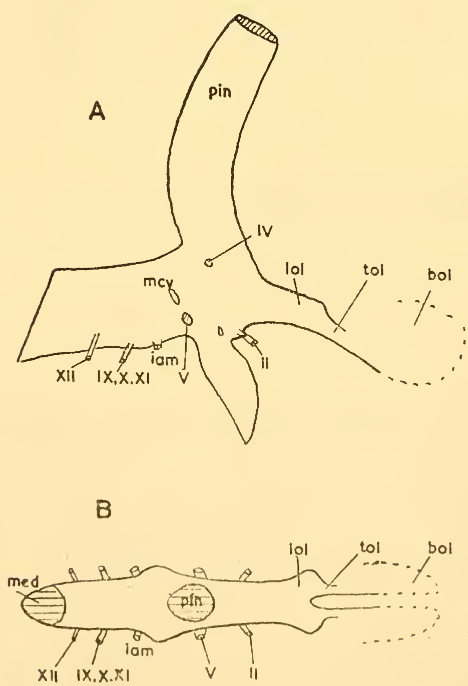


Fig. 16. *Mormosaurus* sp. S.A.M. 12060 × ¼.
Outline drawings of the endocranial cavity reconstructed from sections. A. Lateral view. B. Dorsal view with the root of the pineal mass seen in section.

and a process of the paroccipital forms the postero-lateral border and the proötic the upper border.

The rostrum is short and low.

The endocranial cavity (Fig. 16)

From the cross-sections I have graphically reconstructed two outline drawings of the endocranial cavity in lateral and dorsal views and on them indicated the exits of the cranial nerves.

The parietal canal is 125 mm in length and the antero-posterior diameter averages 15 mm. Due to its pear-shape the lateral diameter varies greatly—16–55 mm.

The sella turcica is deep, extending downwards for half the height of the parabasisphenoid.

The brain is long, narrow and fairly high.

S.A.M. 11294 *Keratocephalus moloch* (Figs 17–20)

This weathered and incomplete posterior part of a skull was described by me in 1956. My interpretation of the nature of the epipterygoid and proötic have proved to be at fault and will now be corrected. In addition I have now cut a median sagittal section through the specimen which has enabled me to clean the left half of the braincase of matrix and to take an endocranial cast.

Outer view of the braincase (Fig. 17)

Both the left and right sides of the braincase have been adequately exposed. The occipital, otic and sphenoidal regions are fully ossified so that the only opening, in addition to the nerve foramina, is in the lateral wall of the sella turcica. As usual the olfactory bulbs have no ossified lateral wall.

The bones forming the lateral wall are: opisthotic, supraoccipital, proötic and the two sphenoidal bones (orbitosphenoid and septosphenoid). The sphenoidal region rests on a median septum formed by the parasphenoid to which a presphenoid is probably indistinguishably fused.

The supraoccipital has dorsally a well-developed flange extending well anteriorly to meet the orbitosphenoid in a plane well anterior of the trigeminal fenestra. Curving down to form the anterior border of the trigeminal fenestra the supraoccipital meets the ascending pillar of the proötic so that the proötic incisure is closed anteriorly.

In lateral view the proötic is seen to be intimately fused to the anterior face of the paroccipital and supraoccipital. Ventrally the proötic enters the margin of the fenestra ovalis and meets the ascending process of the basisphenoid and together they form the dorsum of the sella turcica. Above the pituitary fossa the proötic meets the orbitosphenoid and here we find the outer opening for the facial nerve (VII). Further dorsally the ascending pillar of the proötic meets the descending process of the supraoccipital.

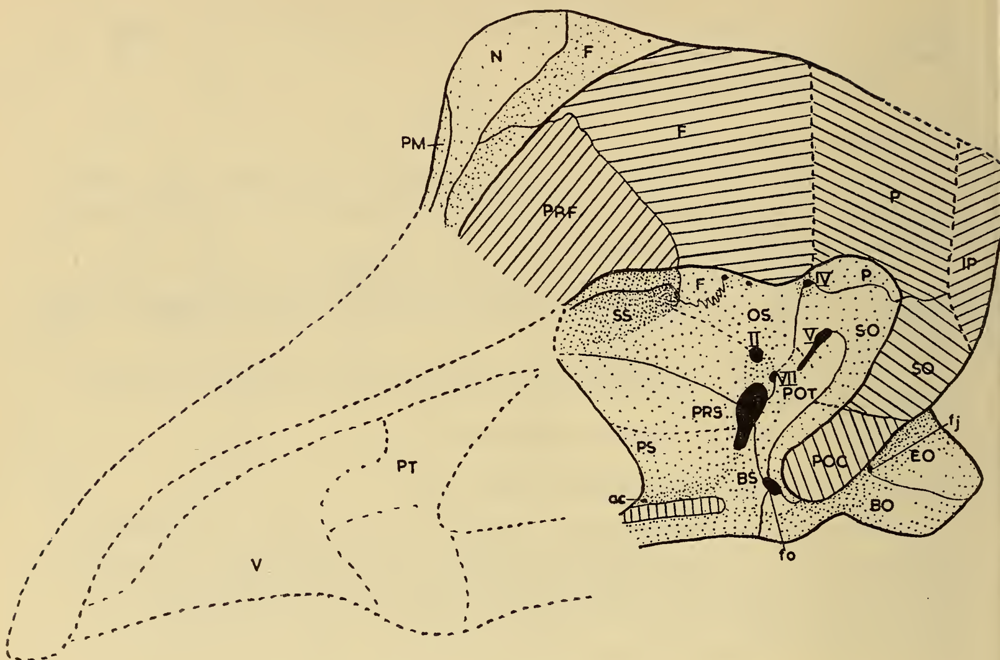


FIG. 17. *Keratocephalus moloch* S.A.M. 11294 × ¼.
Lateral view of the braincase based on the exposed surfaces of both sides, with the occipital and roof-bones shown in reconstructed section.

Orbitosphenoid

The orbitosphenoid has a large lateral face. Its lower part forms a median septum resting on the septosphenoid. Its upper part encloses the diencephalon. Above the pituitary fossa there is a depression to house the Gasserian ganglion. In the upper part of this hollow lies a large rounded foramen for the optic nerve (II).

The orbitosphenoid is applied to the under surface of the frontal. Here lie two fairly small foramina. At the junction of orbitosphenoid, supraoccipital, frontal and parietal there is another foramen. This is probably for the trochlearis (IV) and one of the anterior foramina for the oculomotorius (III).

Septosphenoid

The septosphenoid forming the upper part of the median unpaired interorbital septum rests on the presphenoidal and ?parasphenoidal part of the interorbital septum.

Dorsally it meets the lower edges of the orbitosphenoidal wings and is applied to and intercalated between the frontals.

Its lateral face carries a longitudinal groove in which the olfactory bulb is housed.

Further back it also forms the floor of the tubes housing the olfactory tracts.

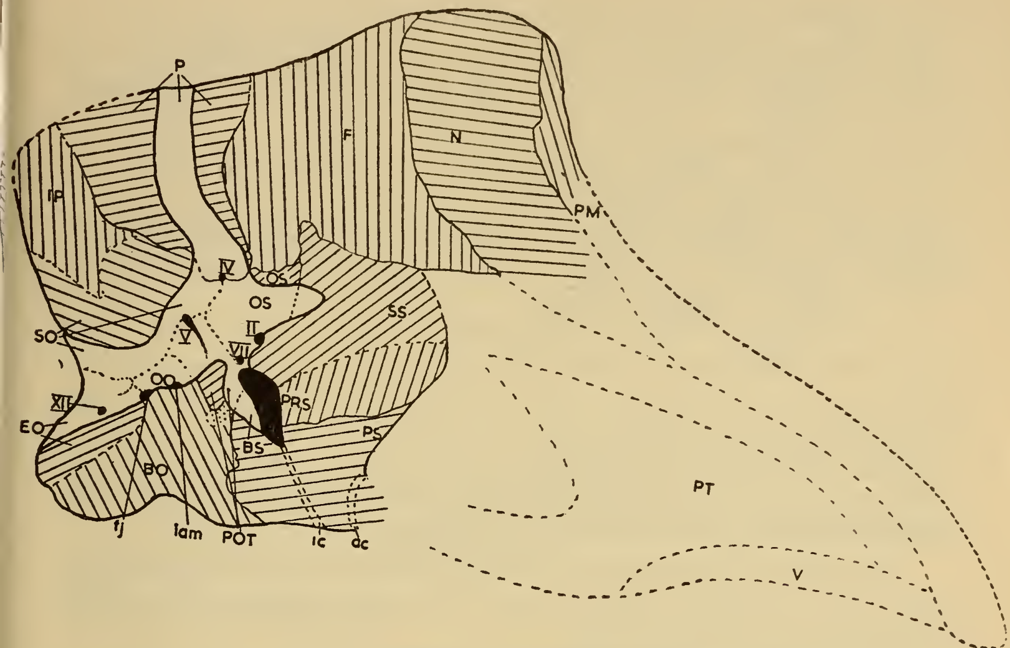


FIG. 18. *Keratocephalus moloch* S.A.M. 11294 × ¼.
The sagittal view of the braincase drawn directly from a sagittal section and the left half of the cleaned endocranial cavity.

Inner view of braincase (Fig. 18)

After cutting through the skull in the sagittal plane I have removed the matrix filling the left half of the endocranial cavity.

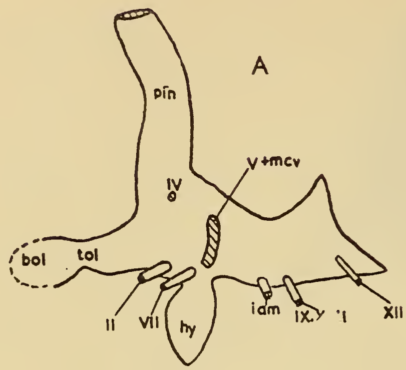
The floor of the braincase is formed by the exoccipital, basioccipital, proötic, basisphenoid, presphenoid, orbitosphenoid and septosphenoid.

The lateral wall is formed by the exoccipital, supraoccipital, opisthotic, proötic, orbitosphenoid and septosphenoid. The parietal organ lies wholly in the parietals.

The roof is formed by the supraoccipital, orbitosphenoid and septosphenoid. The hypoglossal foramen through the exoccipital, the jugular foramen bounded by the exoccipital and opisthotic, the internal auditory meatus into the opisthotic, the facialis foramen through the proötic and the optic foramen through the orbitosphenoid all lie low down, mostly at floor level. The trigeminal fenestra bounded by the proötic and supraoccipital lies well up in the side wall and the trochlear foramen bounded by the supraoccipital, parietal and orbitosphenoid lies near the root of the parietal organ.

The dorsum sellae has its lower half formed by the basisphenoid and its upper half by the proötic. The frons sellae is formed by the presphenoid and septosphenoid.

The parietal tube is 108 mm high, with maximum diameters 30 × 60 mm.



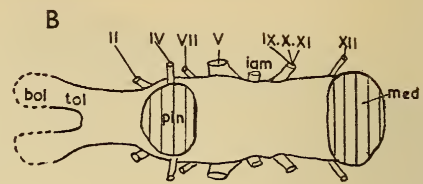


Fig. 19. *Keratocephalus moloch* S.A.M. 11294 × ¼. A cast taken of the left half of the cleaned endocranial cavity. A. Lateral view. B. Dorsal view.

Cast of the endocranial cavity (Fig. 19)

The cavity is short and as high as it is wide. The exits for nerves II, VII, VIII, IX, X and XI and XII are at floor level. The trigeminal fenestra lies well up the side and that of the trochlearis very high up.

The olfactory tract was short, the olfactory lobes and cerebral hemispheres were small: the chiasma is faintly indicated as a cross swelling at the level of the emergence of the optic nerves.

The presence of a flocculus is faintly indicated.

S.A.M. 12093 *Keratocephalus* sp. (Fig. 20)

This skull lacks the basicranial axis, but dorsally of this it is quite well preserved. After cutting it through in the sagittal plane I have been able to clean both halves of the endocranial cavity of matrix.

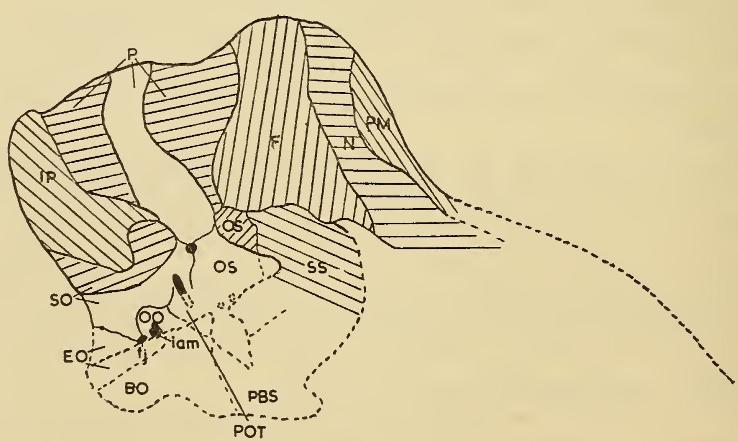


Fig. 20. *Keratocephalus* sp. S.A.M. 12093 × ¼.
Sagittal view of the dorso-posterior part of a skull sectioned in the median plane and after cleaning the endocranial cavity.

The sutures between the constituent bones of the braincase as shown in the accompanying figure are clearly shown. It is quite definite that the septosphenoid forms a median septum lying dorsally between the olfactory tracts and the olfactory bulbs.

The orbitosphenoid forms the roof and sides of that part of the braincase enclosing the thalamus and cerebral hemispheres.

The parietal canal is curiously curved; its height is 100 mm: the greatest antero-posterior diameter is 32 mm but it is greatly expanded from side to side with the greatest diameter 48 mm.

S.A.M. 11972 *Moschops capensis* (Figs 21–26)

This specimen, consisting of a good posterior two-thirds of a skull, was described and figured by me in 1957.

I have now cut out the median part of the skull as a rectangular block and of this block I have cut a series of 120 cross-sections in order to study the detailed structure of the braincase and the supporting bones.

I am publishing here some of the cross-sections and a number of figures reconstructed from these serial sections.

Outer view of braincase (Fig. 21)

In the figure the right side of the braincase is seen in lateral view and the bones of the occipital plate and the dermal bones of the skull-cap are seen in

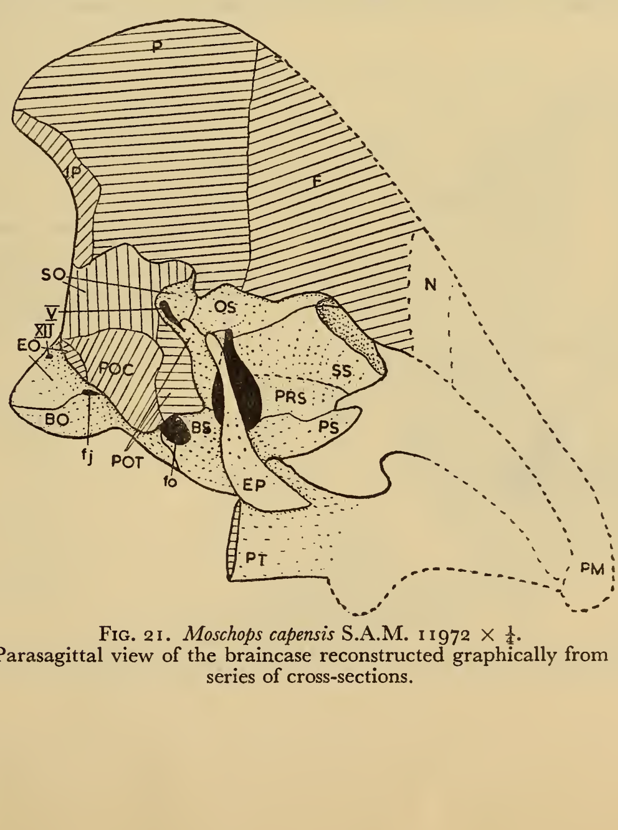


Fig. 21. *Moschops capensis* S.A.M. 11972 × ¼.
Parasagittal view of the braincase reconstructed graphically from a series of cross-sections.

parasagittal section.

It is clear that the lateral wall is well ossified; anteriorly the olfactory region has no lateral bony wall; in the middle the metoptic fissure is still widely patent, except dorsally where it is closed through the junction of the ossifications of the otic and sphenoidal regions. Noteworthy is the great anterior extent of the lateral flange of the supraoccipital. This, together with the great forward growth of the proötic, closes the trigeminal incisure with a wide sheet of bone ossified in the pila antotica, but the trigeminal fenestra, through which passes the median cerebral vein and the trigeminal nerve is still large.

Laterally to the persistent metoptic fissure lies the slender upper part of the epipterygoid, forming above a roomy cavum epiptericum. There is no posterior process to the footplate of the epipterygoid. When fully developed the epipterygoid would dorsally extend to meet the downwardly directed flange of the parietal.

The median septum of the pterygoid is not fully developed in this specimen; but in the American Museum of Natural History there is a specimen figured by me in which the pterygoid septum makes contact with the tip of the parasphenoidal rostrum.

The fenestra ovalis lies low down in the skull with its rim formed by the basioccipital, parabasisphenoid, opisthotic and proötic.

The braincase in sagittal view (Fig. 22)

In sagittal section it is evident that the brain rests on the exoccipitals, basioccipital, proötics, basisphenoid and the sphenoids. Laterally the brain is

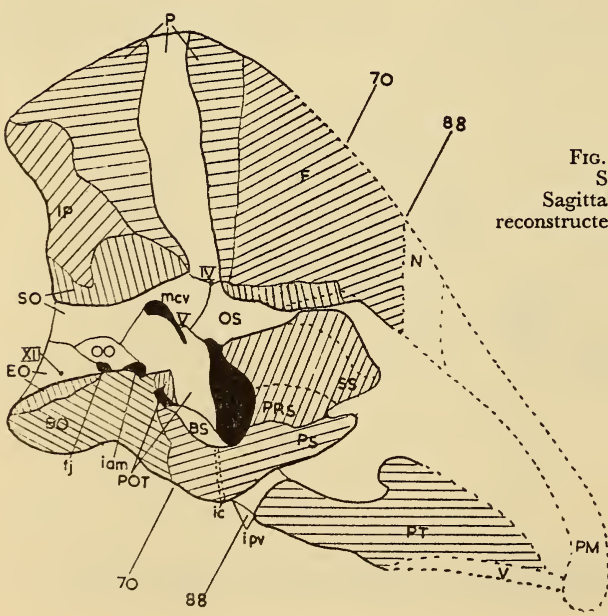


FIG. 22. *Moschops capensis* S.A.M. 11972 × ¼. Sagittal view of the braincase reconstructed graphically from a series of cross-sections.

bounded by the following bones: exoccipital, supraoccipital, opistothotic, proötic and orbitosphenoid. The roof to the brain is formed by the supraoccipital, frontal, and orbitosphenoid.

Internally the openings for the hypoglossal, the foramen jugulare and the internal auditory meatus lie low down on the sidewall at floor level.

The upper part of the dorsum sellae is formed by the proötics meeting each other in the median line. The lower part of the dorsum sellae is formed by the basisphenoid.

The IVth nerve lies high—at the root of the parietal organ.

The orbitosphenoid is a small bone intercalated between the frontals in the median line and forms part of the roof of the rhienecphalon.

In its upper part the orbitosphenoid posteriorly encloses the olfactory lobes, and further forward forms a pair of tubes to house the tracti olfactorii and anteriorly the septosphenoid forms grooves opening laterally to house the olfactory bulbs.

The lower part of the sphenoid complex forms a median septum and this part would appear to be composed of a septosphenoid and a presphenoid resting on the upper edge of the parasphenoidal rostrum.

The parietal tube is large with a height of 130 mm. Its sides are irregular with diameters varying from 16 to 34 mm.

The basicranial axis (Fig. 23)

The basicranial axis is formed by the firmly united exoccipitals, basioccipital and the fused parabasisphenoid.

In ventral view it is evident that the fenestrae ovales lie very close to the median line. Only the posterior part of the interpterygoid vacuity is patent with the result that the parasphenoidal rostrum is obscured by the pterygoids meeting in the median line. The parabasisphenoid is firmly joined to the epipterygoid and the footplate of the epipterygoid but, though immovable, the old basiptery-

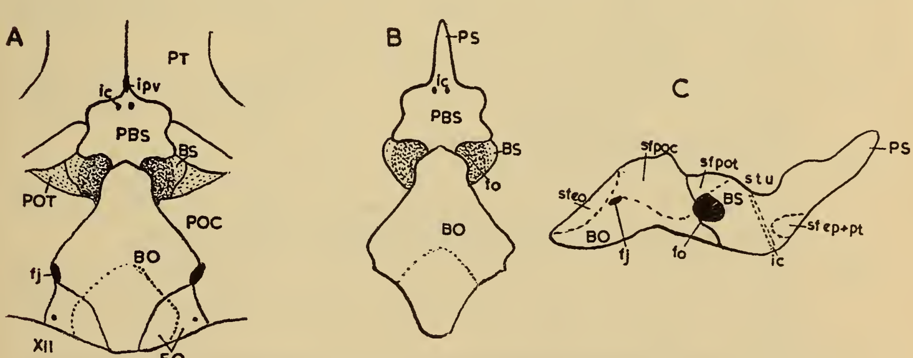


Fig. 23. *Moschops capensis* S.A.M. 11972 × ¼.
The basicranial axis reconstructed from cross-sections. A. Ventral view in relation to supporting bones. B. Vental view. C. Lateral view.

goidal process of the basisphenoid is still defined.

In lateral view it is seen that the parasphenoidal rostrum is directed upwards at an angle of 45° to the cranial base.

The endocranial cavity (Fig. 24).

From the series of cross-sections I have graphically reconstructed outline drawings of the endocranial cavity in lateral and dorsal views.

The parietal organ is enormous, but the large size indicated for the hypophysis is due to the fact that the ossification of both the dorsum and frons of the sella turcica is incomplete.

The telencephalon appears to have been weakly developed.

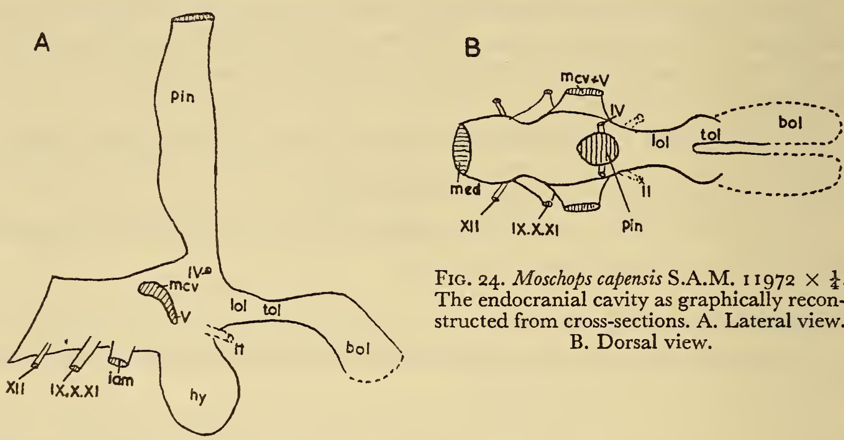


FIG. 24. *Moschops capensis* S.A.M. 11972 × ½. The endocranial cavity as graphically reconstructed from cross-sections. A. Lateral view. B. Dorsal view.

The sphenoidal complex (Fig. 25)

In the accompanying figure some cross-sections through the sphenoidal region show the relations of the constituent elements.

70. At the level of the olfactory lobe the orbitosphenoids in section present a Y enclosing the brain from below, above and from the sides. Dorsally they abut against the lower face of the frontals.

74. 10 mm anteriorly the septosphenoid is Y-shaped and dorsally abuts against the orbitosphenoid, which is a small elongated median bone intercalated between the two frontals.

80. 14 mm anteriorly the brain forms a pair of olfactory tracts separated by a median pillar formed of the septosphenoid. Above this there is still an orbitosphenoid which has become narrower and shallower.

82. 5 mm further forward there is still a narrow orbitosphenoid and the olfactory bulbs are exposed laterally. The septum formed by the septosphenoid is greatly thickened.

88. The obitosphenoid has terminated and the upper part of the septum is still wide, whereas the lower part is narrow and may represent a presphenoid. This rests on the parasphenoidal rostrum.

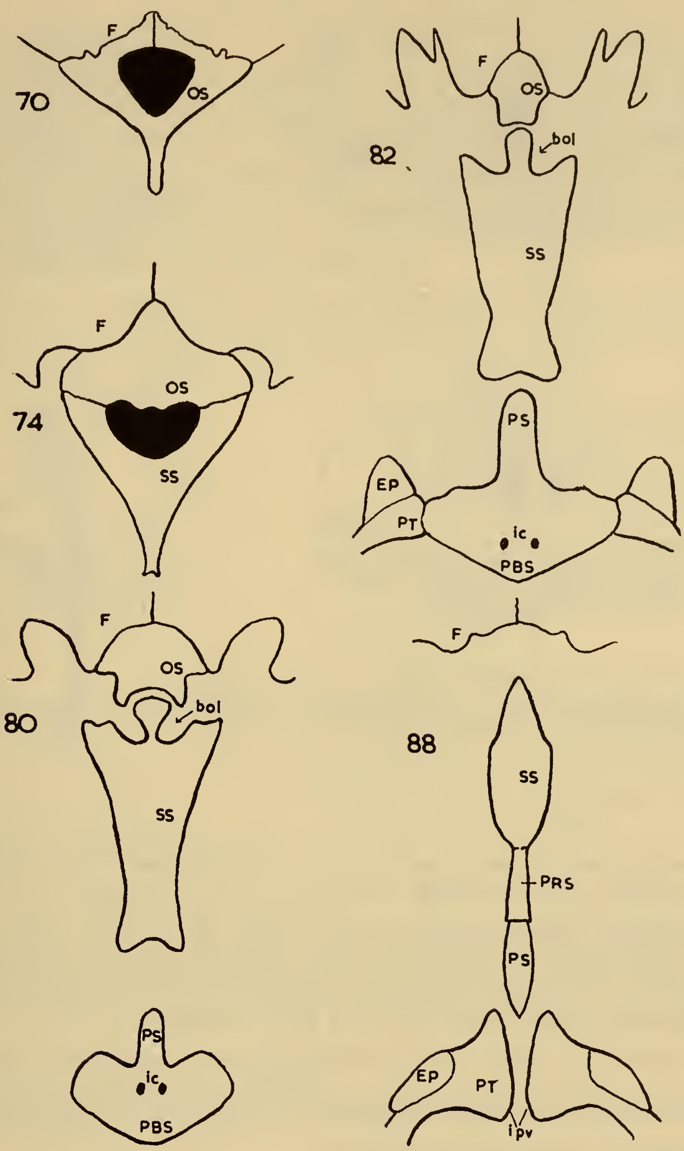


FIG. 25. *Moschops capensis* S.A.M. 11972 × ½
A series of sections through the sphenoidal region from back to front.

S.A.M. 11985 *Moschops* sp. (Fig. 26)

This specimen consists of a very well-preserved isolated occipital plate.

In posterior view (A) the tripartite nature of the condyle is well shown, with the basioccipital lower third forming the articular face so that the skull

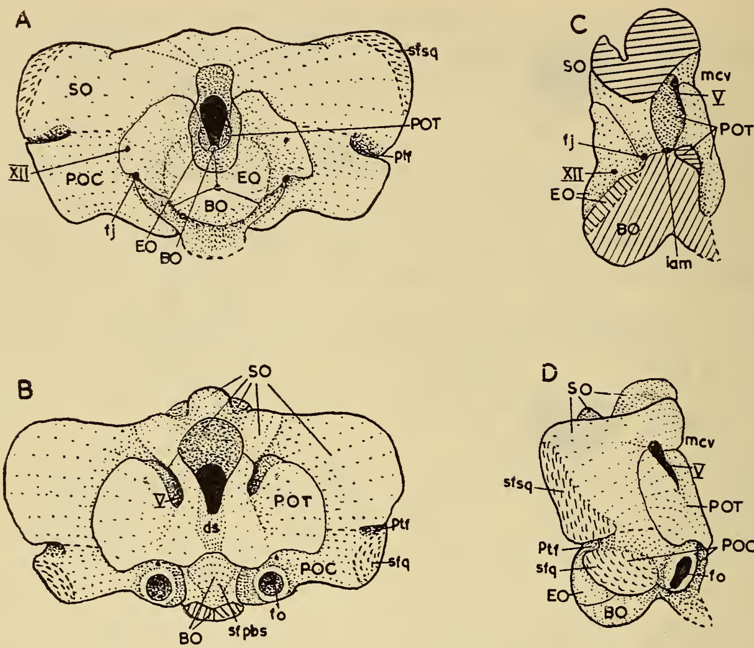


FIG. 26. *Moschops* sp. S.A.M. 11985 × ¼.
An isolated occipital plate. A. Posterior view. B. Anterior view. C. Sagittal view. drawn after the endocranial cavity had been cleaned. D. Parasagittal view.

would hang down at a sharp angle. The exoccipitals meet in the median line to form the floor for the medulla. Anterior to the exoccipitals a hump in the floor is formed by the basioccipital lying between the internal auditory meati.

In anterior view (B) the proötics are seen lying intimately applied to the anterior face of both supraoccipital and opisthotic. They meet in the median line, where they are hollowed out and form the upper part of the dorsum sellae. Dorsally the proötic has an ascending pillar, which meets a descending process of the supraoccipital. These are ossifications in the pila antotica and enclose the trigeminal fenestra anteriorly. Lateral to the trigeminal fenestra lies the foramen for the VIth cranial nerve.

Below each proötic lies the circular fenestra ovalis, which forms a cup-shaped depression in the opisthotic pierced by two foramina leading into the internal auditory meatus.

The hollow is bounded by a sharp raised rim formed by the opisthotic. The parabasisphenoid has fallen away, but when present the basisphenoid together with the basioccipital and proötic form an outer rim to the fenestra ovalis which partly obscures the inner rim formed solely by the opisthotic.

Between the lower edge of the proötic and the fenestra ovalis lies the opening of the VIIth cranial nerve.

In sagittal section (C) it can be seen that the braincase floor is formed by the exoccipital, basioccipital and proötic, with the foramen for the XIIth, the jugular foramen and the internal auditory meatus lying at floor level.

Piercing the ascending process of the proötic is the foramen for the VIth nerve. Behind the proötic-supraoccipital bar lies the slit-like trigeminal fenestra. Behind this the sidewall of the braincase, here formed by the proötic, is hollowed out and in this hollow the flocculus was housed.

In (D) the occipital plate is seen in lateral view and shows the slit-like trigeminal fenestra bounded anteriorly by the proötic and supraoccipital and the fenestra ovalis bounded by a rim formed by the opisthotic.

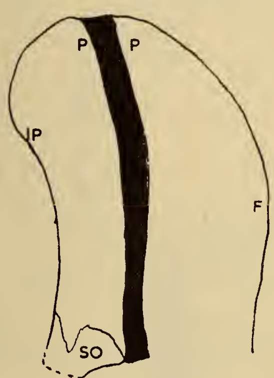


FIG. 27. *Criocephalus* sp.
S.A.M. 11701 × ¼.
Sagittal section through the skull cap showing the pineal tube.

S.A.M. 11701 *Criocephalus* sp. (Fig. 27)

A sagittal cut through this skull-cap shows the constituent bones to be of cancellous nature and the fusion of these spongy bones has obliterated nearly all traces of the original sutures between them.

The parietal tube is curved and lies parallel to the midline of the occiput and the curvature of the dorsal surface of parietal and frontal. It is very long—185 mm, the antero-posterior diameter varies from 9 to 14 mm.

S.A.M. 12046 *Criocephalus* sp. (Fig. 28)

A sagittal section cut through a badly weathered skull-cap shows the great thickness of the parietal bone with the parietal tube penetrating this bone. The tube measures 240 mm in height and the diameters vary from 15 to 20 mm.

S.A.M. 12066 *Criocephalus* sp. (Fig. 29)

A sagittal section through this skull-cap shows the limits of the constituent bones, although they are spongy.

The parietal tube runs nearly parallel to the midline of the occiput. Its length is 198 mm and the antero posterior diameter varies from 16 to 23 mm.

S.A.M. K268 *Criocephalus gunyankaensis* (Fig. 30)

Four of the skull-caps, described in 1946, are here figured.

A. In this specimen most of a natural cast of the parietal tube is preserved as well as the tube itself. The length of the tube is 310 mm. At its dorsal

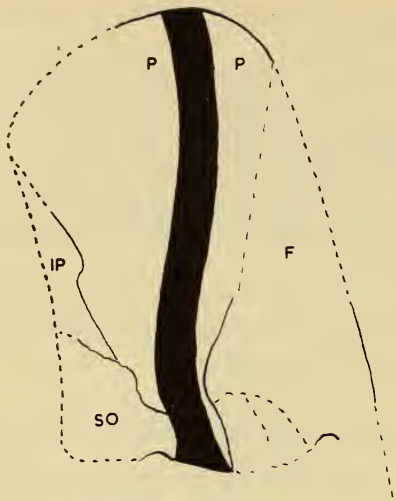


Fig. 28. *Criocephalus* sp.
S.A.M. 12046 × ¼
Sagittal section through the pineal tube.

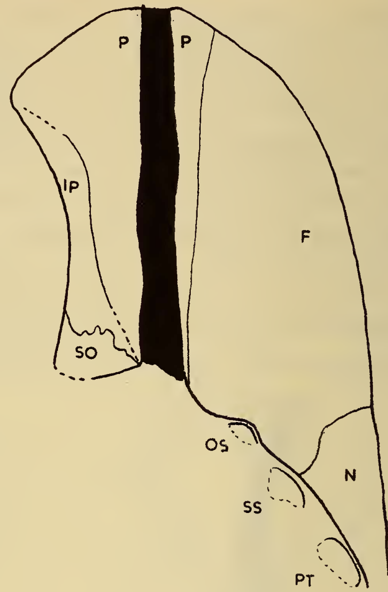


Fig. 29. *Criocephalus* sp.
S.A.M. 12066 × ¼.
Sagittal section through the skull cap.

extremity the cast is oval in cross-section with diameters 22 × 27 mm. The skull bones are very spongy, but the face of the tube is very smooth and is formed of dense and compact tissue.

B. I have cut a frontal section through the parietal tube of this specimen. The tube is 306 mm in length and the side to side diameter varies from 17 to 26 mm. No sutures in the surrounding cancellous bone can be determined.

E. A natural longitudinal fracture passes through the parietal tube, whose length as reconstructed is 308 mm with antero-posterior diameters varying from 16 to 25 mm.

F. A longitudinal cut has been made through the skull to give a sagittal section of the parietal tube which has a length as reconstructed of 170 mm and antero-posterior diameters varying from 17 to 26 mm.

ANTEOSAURIA

S.A.M. 9085 }
S.A.M. 12082 } *Anteosaurus* sp. (Figs 31–37)

As S.A.M. 12082 lacks the anterior end of the snout I have sectioned a snout S.A.M. 9085 and from these combined I have graphically reconstructed the skull from two views.

S.A.M. 12082 was contained in a sandstone bed of about 24 inches. Much of the upper surface of the skull was weathered away and the rest contained in a

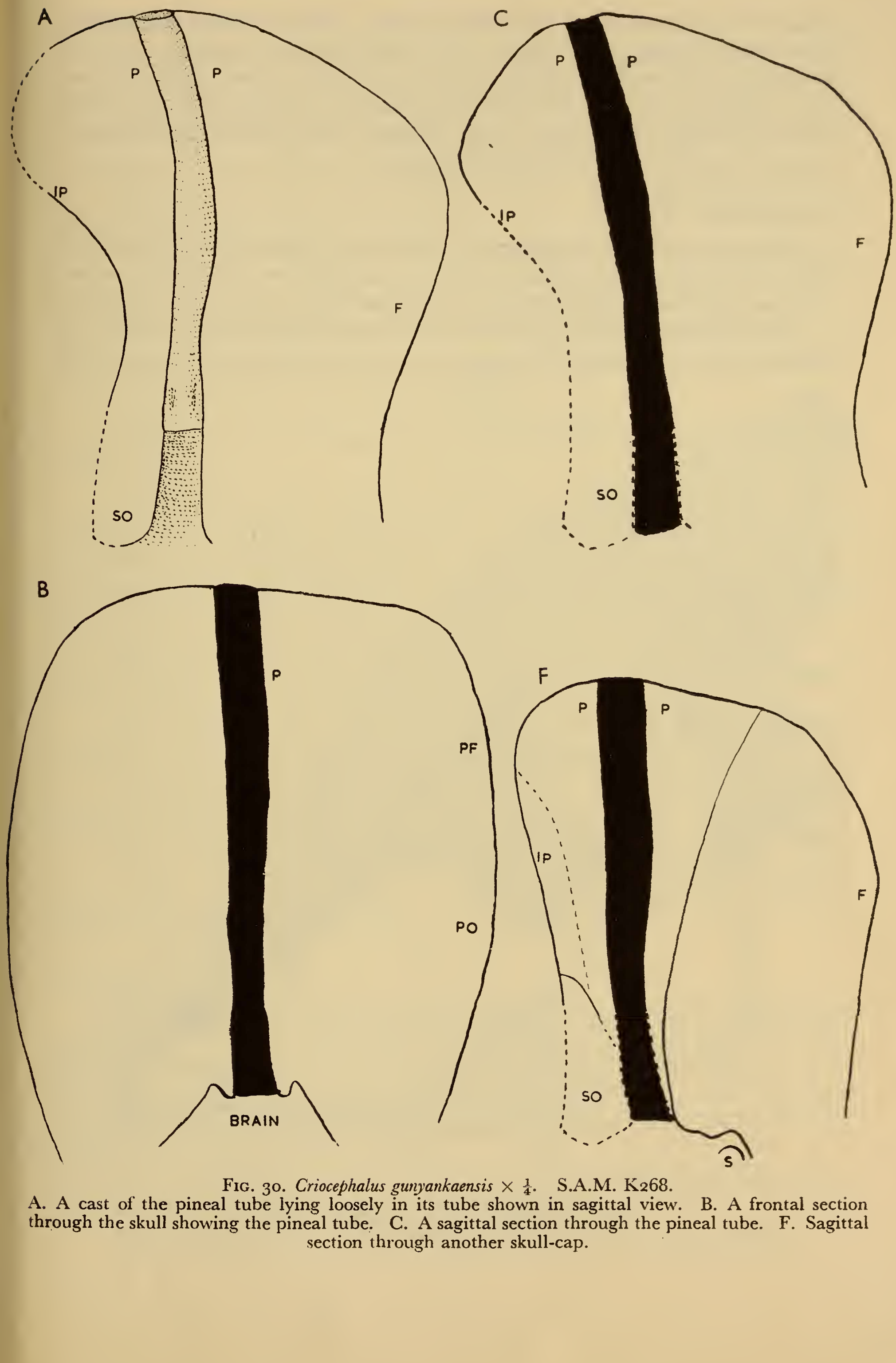


FIG. 30. *Criocephalus gunyankaensis* × $\frac{1}{4}$. S.A.M. K268.
A. A cast of the pineal tube lying loosely in its tube shown in sagittal view. B. A frontal section through the skull showing the pineal tube. C. A sagittal section through the pineal tube. F. Sagittal section through another skull-cap.

number of blocks weathered at the fracture faces. Unfortunately these fractures have passed through vital regions of the skull. So that, although the well-preserved parts have given excellent sections, a number of structural features are indeterminable and some doubtful. However, the reconstructions give a fair picture of the internal structures of the anteosaur skull and profitable comparisons can be made with the other Dinocephalia.

Parasagittal view (Fig. 31)

The outer surface of the braincase is formed by the bones found here in all Dinocephalia. Posteriorly the bones of the occipital plate are seen in section. The exoccipital has a large outer face and is pierced by a large jugular foramen.

The supraoccipital sends the usual flange anteriorly to meet the sphenoid complex and a downwardly directed process curving down in front of the

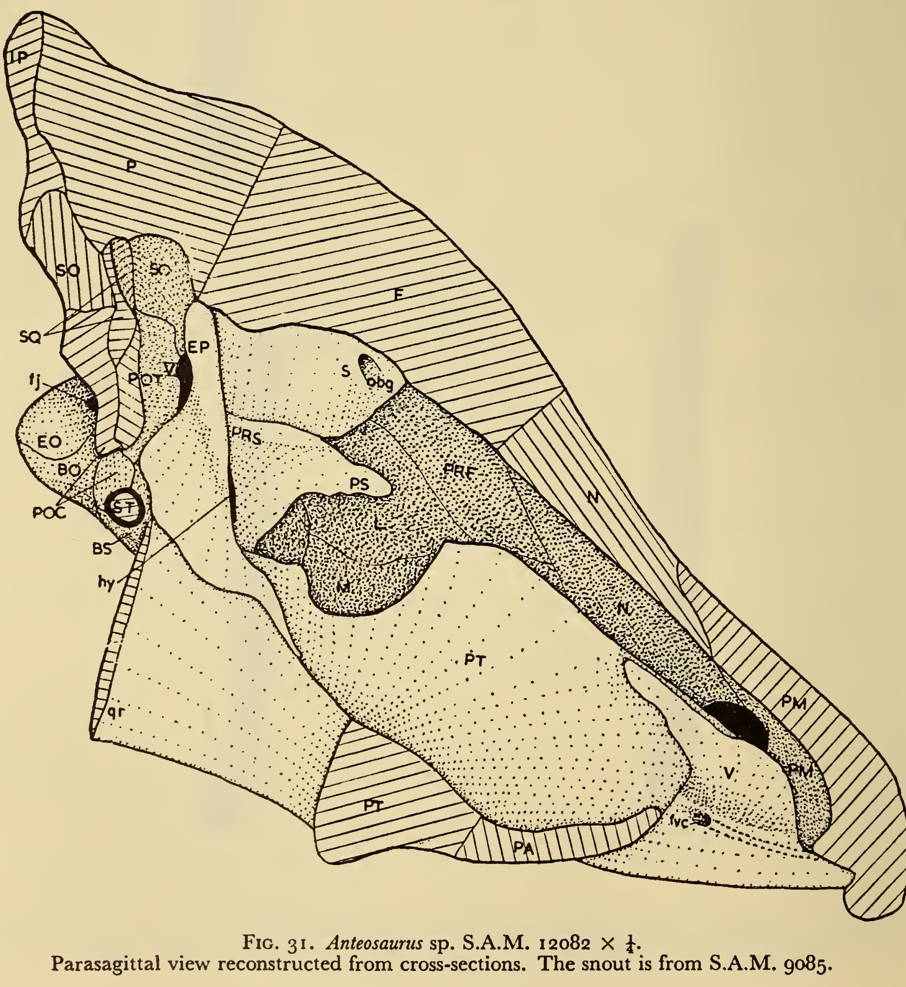


FIG. 31. *Anteosaurus* sp. S.A.M. 12082 × ½.
Parasagittal view reconstructed from cross-sections. The snout is from S.A.M. 9085.

trigeminal fossa.

The proötic, as ossified, is of small postero-anterior extent. Its anterior margin carries a trigeminal notch. In maturity, I believe, that the antotic pila, here cartilaginous, would be ossified.

Of the foramina for the cranial nerves I have only been able to determine the position of the trigeminal nerve and the jugular foramen.

The fenestra ovalis is large and lies low down, with its borders formed by the opisthotic, basisphenoid and the proötic.

The sphenoid complex is of the usual dinocephalian nature, but the limits of the orbitosphenoid and septosphenoid cannot be wholly determined. The open groove in the septosphenoid for the olfactory bulb is small.

Below the sphenoid complex lies the median septum formed chiefly by the parasphenoid. A distinct presphenoid cannot be determined but would form the postero dorsal corner above the parasphenoid.

As preserved the lateral wall has a large fenestra due to the fact that the trigeminal fenestra is not closed anteriorly and is thus confluent with the hypophyseal fenestra.

Lying lateral to this is the very well-developed epipterygoid. The footplate resting on and wedged in the pterygoid and the basisphenoid is very well developed and of great antero-posterior extent, but without a posterior process. The ascending process is only moderately expanded, but is very strong. Its upper part and the upper anterior border are greatly thickened. In section this thickening presents a strong bulbous knob (fig. 36).

The median septum of the snout is strongly developed but the ossification fails to reach the interorbital septum dorso-posteriorly.

It is mainly composed of well-developed sheets of the pterygoids and only anteriorly is the pterygoidal septum flanked by sheets from the vomers.

Posteriorly the pterygoids, in the region of the inter-pterygoidal vacuity, have the septal sheets widely separated to enclose a roomy trough. Further anteriorly the pair of sheets approach one another and finally coalesce (fig. 35).

Where the interchoanal vomerine bar curves inwards to the median septum there is the usual groove leading into the vomerine tunnel which carries a branch of the naso-palatine nerve.

Sagittal view (Fig. 32)

Due to poor preservation the details of the internal structure of the endocranial cavity could not be determined. The general structure is, however, in essentials very similar to that of the other Dinocephalia. The endocranial cavity is relatively small and short. The proötic is not ossified anterior to the trigeminal notch; it, however, meets its fellow in the median line and forms the upper part of the dorsum sellae.

Above the interpterygoid vacuity the two pterygoidal median sheets arise well lateral to the median line and form a deep trough.

The parasphenoidal septum is fairly weak.

The basicranial axis (Fig. 33)

Except that it is rather broad the axis has the same structural plan as the other Dinocephalia. The fenestra ovalis is situated very low down and the parasphenoidal septum stands practically vertically to the long axis, with its posterodorsal corner probably formed by the presphenoid.

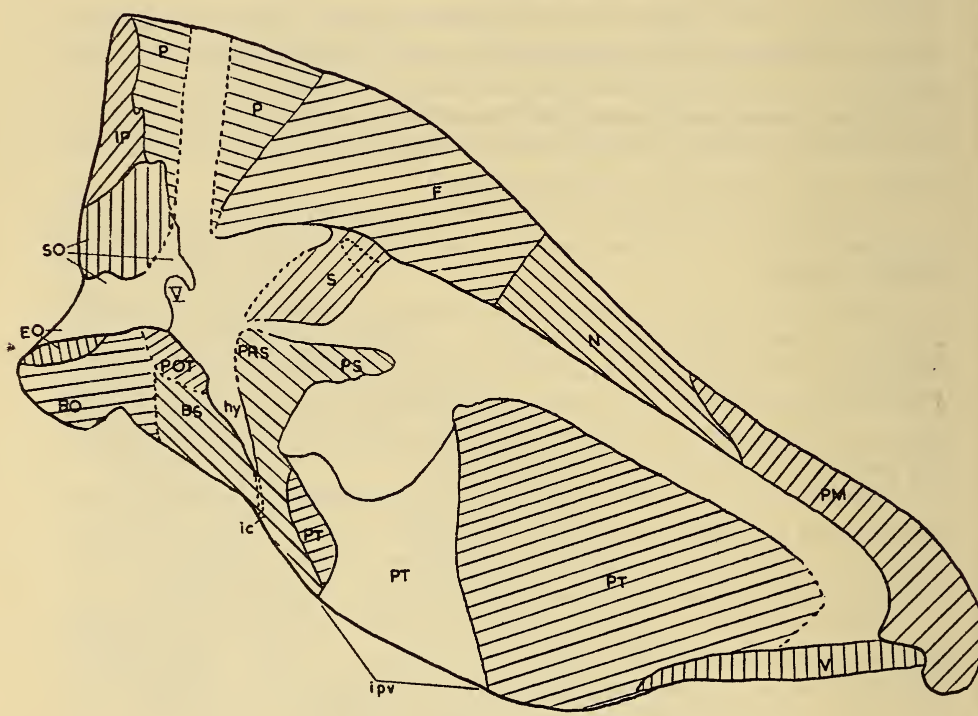
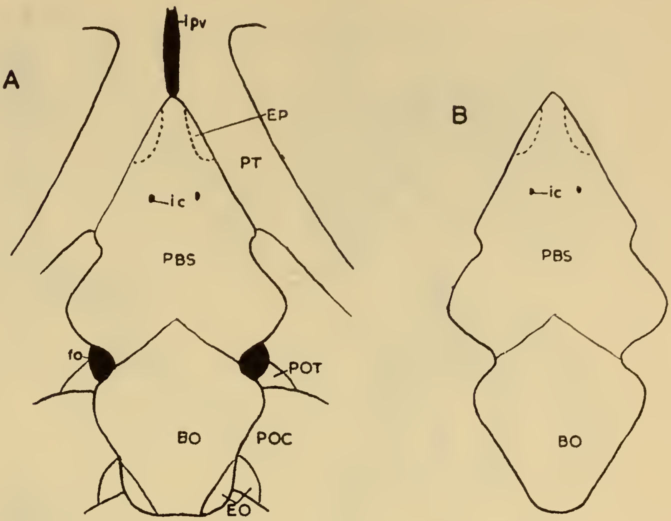


FIG. 32. *Anteosaurus* sp. S.A.M. 12082 and S.A.M. 9085 × ¼.
Sagittal view reconstructed from cross-sections.

Cross-sections through septum of the snout (Fig. 34)

1. This section across the anterior end of the choanae shows the premaxillary processes overlying the anterior end of the vomers. The tunnel for the naso-palatine nerve branch lies between the vomer and premaxillary process. The pterygoid does not meet the premaxilla.
2. Shows the groove on the lateral surface of the vomer for the entry of a branch of the naso-palatine nerve.
3. Near the posterior end of the choanae the fused pterygoidal septum is



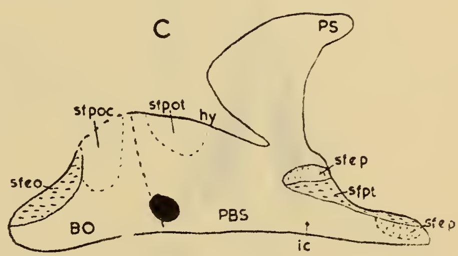


FIG. 33. *Anteosaurus* sp. S.A.M. 12082 × ½. The basicranial axis graphically reconstructed from cross-sections. A. Ventral view in relation to supporting bones. B. Ventral view. C. Lateral view.

seen flanked by the vomerine septa. A cavity separates the middle portions of the pterygoidal and vomerine septa.

4. Just posterior to the choanae the postero-dorsal part of the vomerine septa still flank the pterygoidal septum. The palatine is seen to overlie the vomer.
5. The fused pterygoids form a high median septum with the posterior ends of the vomerine septa still flanking it dorsally.

Cross-section through the footplate of the epipterygoid (Figs 35–36).

Part of the ventral region has been destroyed by weathering but enough is preserved to show most of the relations of the epipterygoid to the pterygoid and parabasisphenoid.

42. Near the posterior end of the interpterygoidal vacuity the pterygoids are seen to carry two dorsally directed sheets of bone lying well lateral of the median line.
43. Immediately posteriorly a tongue of the epiterygoid is seen lying in the substance of the pterygoid.

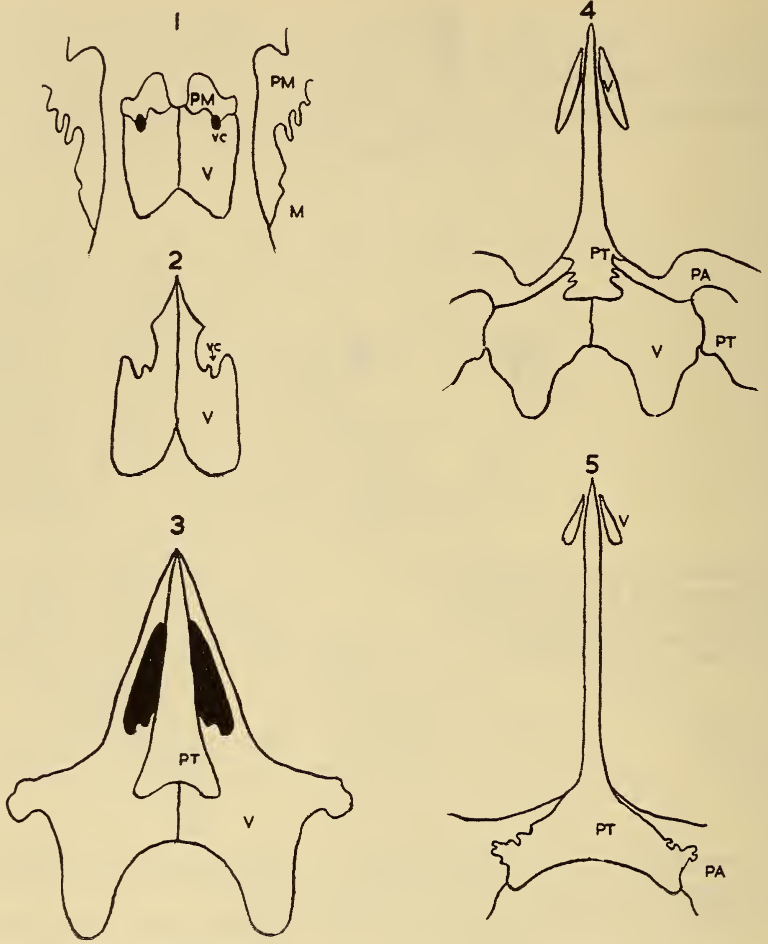


FIG. 34. *Anteosaurus* sp. × ½.
1 and 2 from S.A.M. 9085; 3 to 5 from S.A.M. 12082. Sections across the snout to show the median septum.

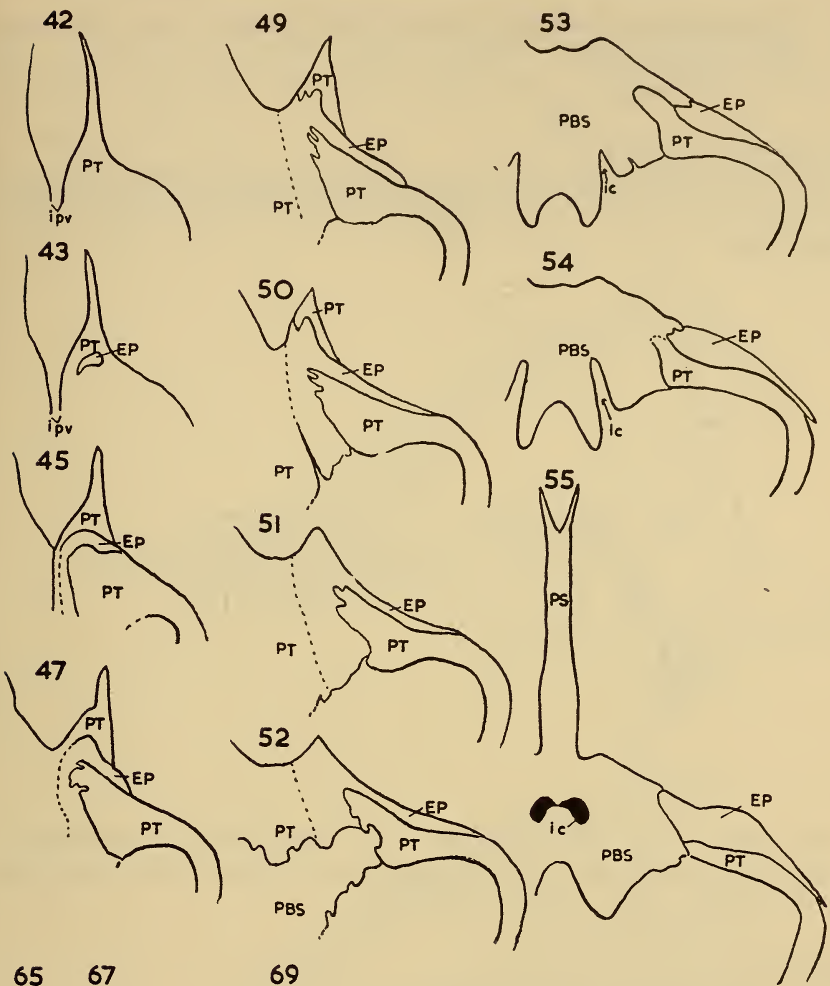
45 & 47. Just posterior to the interpterygoidal vacuity the epiterygoid is seen to extend medially and also ventrally.

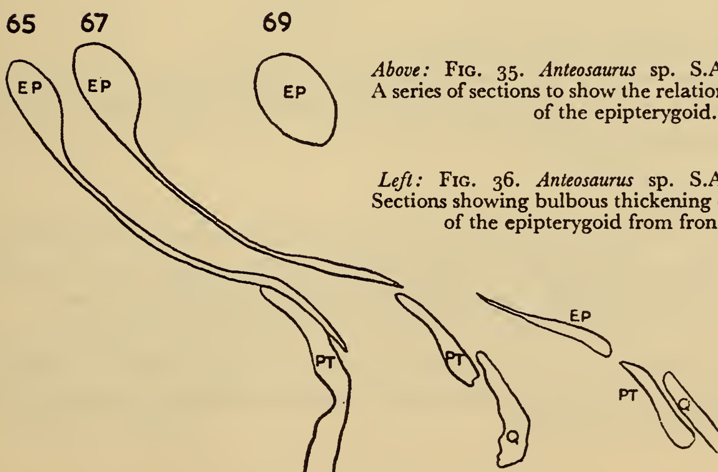
49, 50 & 51. The epipterygoid forms part of the floor of the median trough and apparently also enters the ventral surface.

52. The epiterygoid apparently overlies the anterior part of the basipterygoid process against which the pterygoid is also applied.

53, 54 & 55. The footplate has moved laterally and is applied to the basipterygoid process together with the pterygoid.

65. The footplate of the epipterygoid lies on and over the dorsal edge of the





Above: Fig. 35. *Anteosaurus* sp. S.A.M. 12082 × ½. A series of sections to show the relations of the footplate of the epipterygoid.

Left: Fig. 36. *Anteosaurus* sp. S.A.M. 12082 × ½. Sections showing bulbous thickening of the upper edge of the epipterygoid from front to back.

quadrate ramus of the pterygoid. Note the thickening of the upper edge of the epipterygoid.

67 & 69. The footplate ends without reaching the quadrate.

The endocranial cavity (Fig. 37)

From the cross-sections in this area which has suffered much from weathering along fracture faces I have attempted graphically to reconstruct the endocranial cavity.

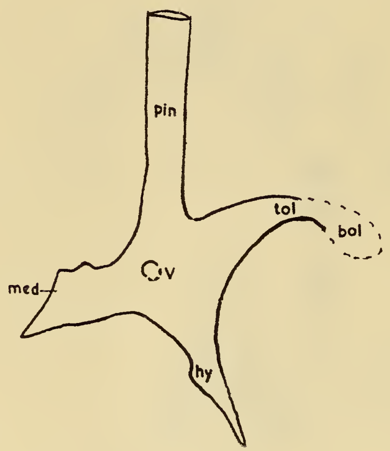


Fig. 37. *Anteosaurus* sp.
S.A.M. 12082 × ¼.
Lateral view of the endocranial cavity in outline.

Few details can be determined but we get some idea of the proportions.

The parietal tube was long—110 mm. The brain could have only been fairly short and low with a small cerebral region.

TITANOSUCHIA

S.A.M. 11486 *Jonkeria* sp. (Figs 38–52)

From a snout a series of 64 cross-sections have been cut and from these reconstructions have been made to show the anterior part of the median septum in sagittal and parasagittal view.

Lateral view (Fig. 38)

The median septum is seen to be formed by the pterygoids rising fairly high in the skull and extending very far anteriorly. The vomer has no dorsal septal development but flanks the pterygoid as a stout interchoanal bar.

The vomerine bar is pierced by a long tunnel. This enters the bone by a foramen from a groove situated fairly high up in the side of the vomer in a plane at the level of the posterior choanal border. It opens anteriorly at the junction of the vomer and the premaxilla.

This tunnel is connected with a shorter tunnel with a separate dorsal entry and a ventral exit foramen. These probably housed branches of the naso-palatine nerve.

Median view (Fig. 38)

The median pterygoid septum is seen to be deeply intercalated between the two vomera and meets the premaxilla.

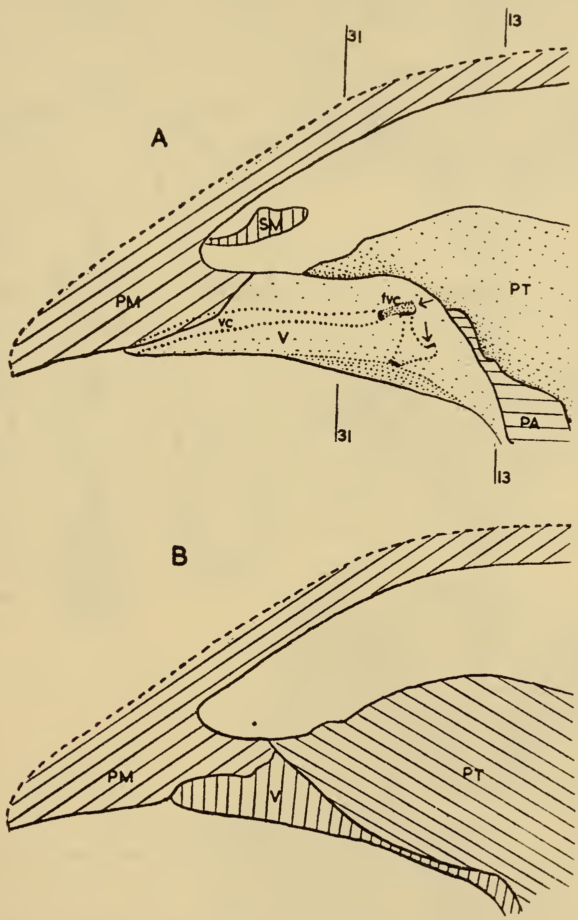


FIG. 38. *Jonkeria* sp. S.A.M. 11486 × ¼.
A. Parasagittal view of the snout reconstructed from cross-sections. B. Sagittal view. 13-13 and 31-31. Region through which the sections, given in the following figure, pass.

Sections (Fig. 39)

Seven sections from front to back show the interesting relations of the component bones.

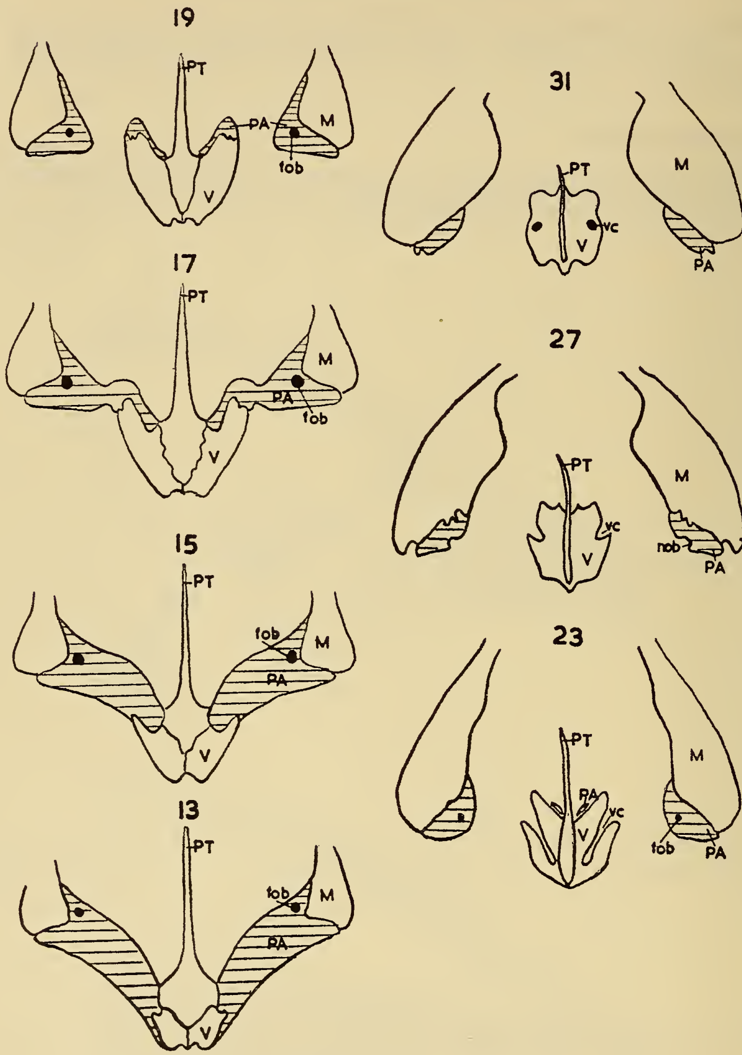


Fig. 39. *Jonkeria* sp. S.A.M. 11486 × ¼.
A series of sections through the median septum of the snout from front to back.

31. Shows the pterygoids as a thin sheet of bone deeply intercalated between the vomers. The tunnel (vc) for the naso-palatine nerve is seen in section.
27. The tunnel opens into a lateral groove. A notch (nob) in the palatine is where the ophthalmic branches of V and VII emerge.
23. Shows the vertical connection between the two tunnels in the vomer. The tunnel for the branches of V and VII is seen penetrating the palatine.

19. The palatine caps the vomer.
17. The palatine overlies the vomer.
15. The palatine meets the pterygoid.
13. The palatine commences to underlie the vomer.

S.A.M. 11556 *Jonkeria* sp. (Figs 40–44)

A poorly preserved skull with most of the outer bones missing has been used to cut a series of cross-sections to reveal the internal structure. The braincase was cut out of the skull in the form of a rectangular block which was then cut across in a consecutive series of 100 sections.

Drawings of some of the sections are here reproduced as also graphically reconstructed sagittal and parasagittal views of the posterior part of the skull and the two outline figures of the endocranial cavity.

The lower surface of the parabasisphenoidal and pterygoidal region has unfortunately suffered from weathering.

Parasagittal view (Fig. 40)

The occiput and dorsal roof-bones are seen in section and the braincase and related bones in lateral aspect.

The trigeminal foramen is anteriorly not closed as the anterior process of the supraoccipital and proötic fail to meet each other. Dorsally it has no border and anteriorly lies the posterior edge of the orbitosphenoid.

Otherwise the proötic is well developed with the foramen for the VIth and VIIth cranial nerves well back from its anterior border.

The sphenoid complex is well developed in its anterior part which is formed

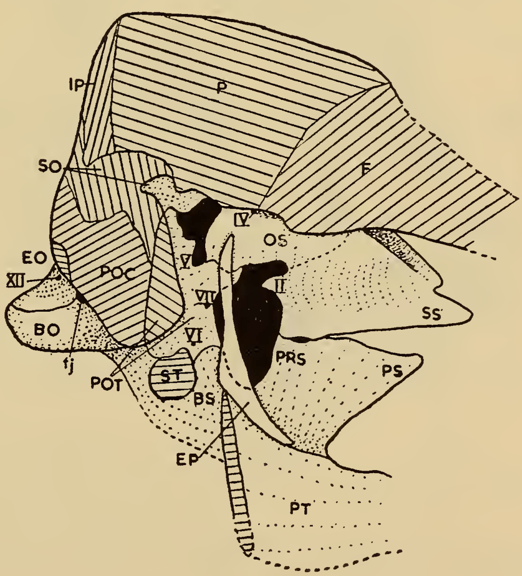


FIG. 40. *Jonkeria* sp. S.A.M. 11556 × ¼. Lateral view of the braincase graphically reconstructed from a series of cross-sections.

by the septosphenoid; its posterior part is less well ossified and it does not meet the supraoccipital and ventrally the orbitosphenoid does not extend so far as to include the optic foramen which therefore pierces cartilage.

Ventrally the septosphenoid has its posterior part supported by the presphenoid. With fuller ossification it would also rest on the parasphenoidal rostum.

The parasphenoid is directed sharply upwards and forwards making with its anterior edge an angle of $\pm$ 70° with the basis cranii.

The postero-dorsal part of the parasphenoidal septum is formed by the presphenoid indistinguishably fused to it.

The epipterygoid has a well-developed footplate, but the ascending process, although nearly reaching the parietal, is slender so that the large lateral fenestra is well exposed.

Sagittal view (Fig. 41)

A sagittal section clearly shows that the present specimen is of an immature reptile. Incomplete ossification is seen in the exoccipital, which only forms part of the posterior floor of the braincase, the incompletely formed dorsum sellae and the large unossified zone in the parabasisphenoid and thirdly the unossified lower part of the orbitosphenoid which does not enclose the optic foramen.

In addition the internal auditory meatus is widely open and the orbitosphenoid is not met by the supraoccipital.

This is the only specimen where there is some indication of the line of

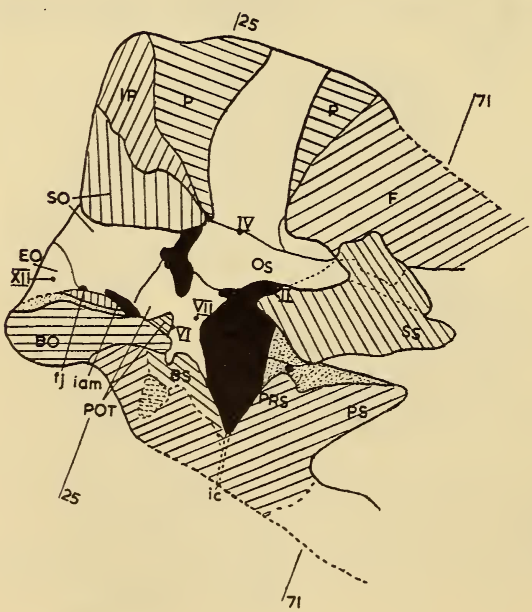


FIG. 41. *Jonkeria* sp. S.A.M. 11556 × ½.
Sagittal view of the braincase as reconstructed. Numbered lines show the plane of the cross-section of the correspondingly numbered sections.

fusion of the basisphenoid to the underlying parasphenoid; but there is no line of junction indicated between the presphenoid and the parasphenoid.

Sections through the posterior part of the braincase (Fig. 42)

25. A section through the plane in which the vestibules lie shows the roof and sides of the braincase formed by the supraoccipital and the floor by the basioccipital.
31. A section through the plane in which the trigeminal foramina lie shows the pair of proötics meeting in the floor of the braincase. Note the imperfect ossification in the parabasisphenoid.

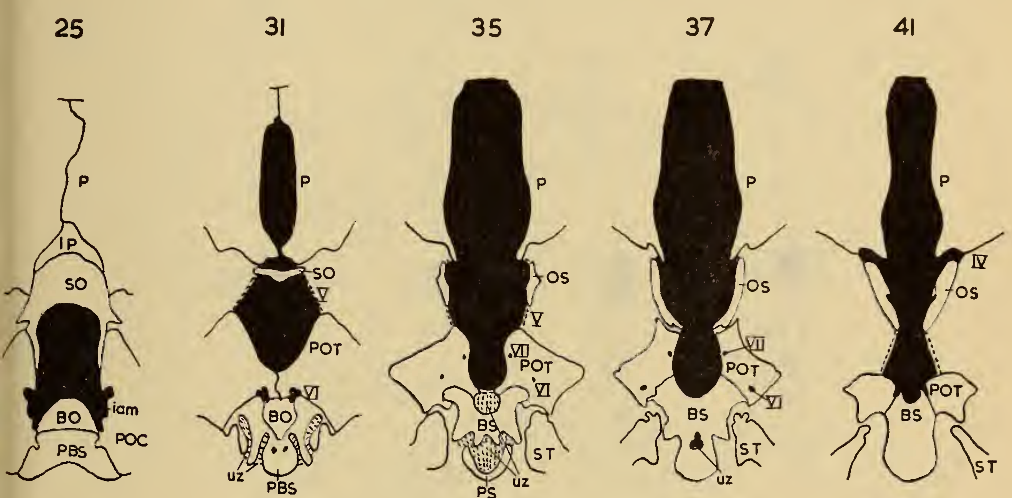


FIG. 42. *Jonkeria* sp. S.A.M. 11556 × ¼.
A selected series of cross-sections through the posterior part of the braincase. Each section bears its number in the consecutive series.

35. This section shows the imperfectly ossified dorsum sellae and an unossified zone between the basisphenoid and the parasphenoid.
37. Here the sidewalls of the braincase are seen to be formed by the orbitosphenoids and the proötics.
41. Lateral to the root of the pineal tube lies the foramen from the IVth cranial nerve and below the orbitosphenoid the sidewall is membranous.

Sections through the sphenoid-complex (Fig. 43)

These cross-sections are from front to back and the line of sections is indicated in figure 41 under the section numbers.

71. In the anterior part of the sphenoid complex the septosphenoid is seen to carry lateral of a median septum grooves which house the paired

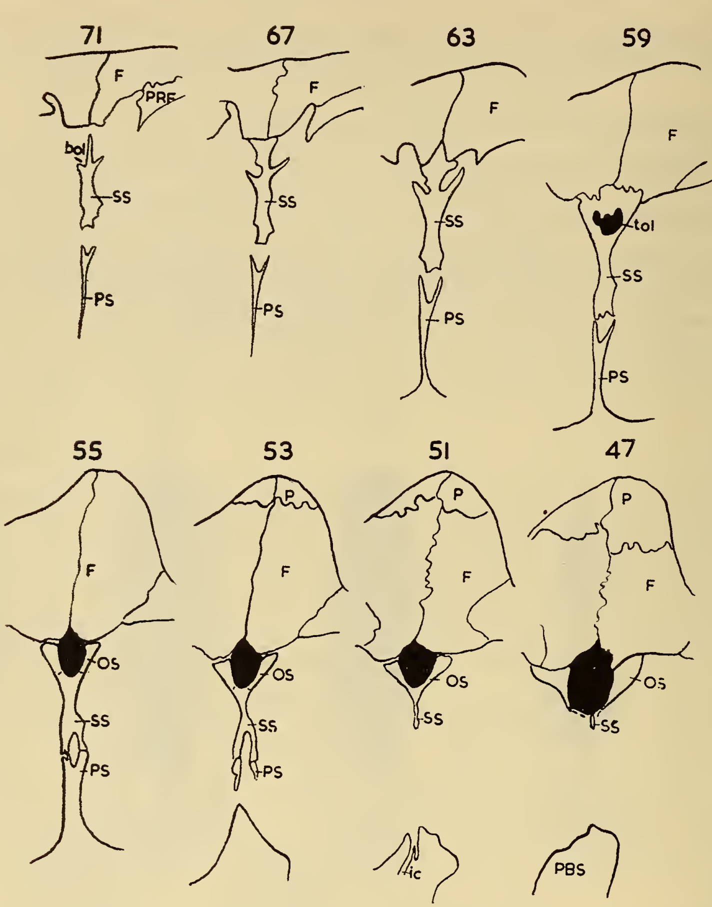


FIG. 43. *Jonkeria* sp. S.A.M. 11556 × ¼.
Sections numbered from front to back through the sphenoidal region.

olfactory bulbs. The forked upper edge of the parasphenoid does not extend to the thickened lower edge of the septosphenoid.

67 & 63. The wings of the septosphenoid curve round the olfactory grooves.

59. The unpaired olfactory tract is enclosed by bone, which may be orbitosphenoid but no break between the wings and the lower septal part can be determined.

55. The lower thickened edge of the sphenoidal septum is forked and meets the upwardly directed fork of the parasphenoid (?presphenoid) to enclose a canal (trabecular canal). The wings enclosing the olfactory lobes appear to be orbitosphenoid.

53. The sphenoidal fork is well developed.

51. In the plane of the perforations for the internal carotids the sphenoidal septum becomes reduced.

47. The sphenoidal septum ends and laterally lie the wings of the orbitosphenoids.

The endocranial cavity (Fig. 44)

In lateral and dorsal outline views of the endocranial cavity the exit points of the various openings and foramina in the braincase are indicated. Of the subdivisions of the brain only the olfactory bulbs, tracts and lobes are clearly demarcated.

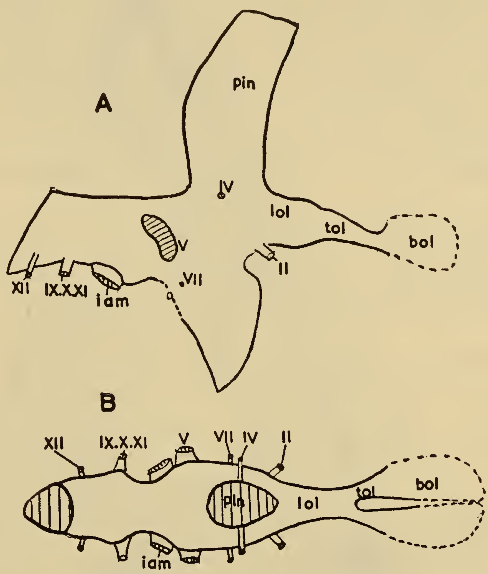


FIG. 44. *Jonkeria* sp. S.A.M. 11556 × ¼.
Outline figures of the endocranial cavity:
a. Lateral view; *b*. Dorsal view.

S.A.M. 11574 *Jonkeria*

Of this fairly good skull I have cut 144 cross-sections. From these I have graphically reconstructed the skull in parasagittal and sagittal section, the basicranial axis in two views and made outline drawings of the endocranial cavity in lateral and dorsal views.

Parasagittal view (Fig. 45)

The lateral wall of the braincase is well ossified and is closed except for a large fenestra in the hypophyseal area and small openings for some of the cranial nerves. Lateral to the olfactory bulbs there is also no bony wall.

Below the anterior part of the braincase there is a fairly well-ossified interorbital septum.

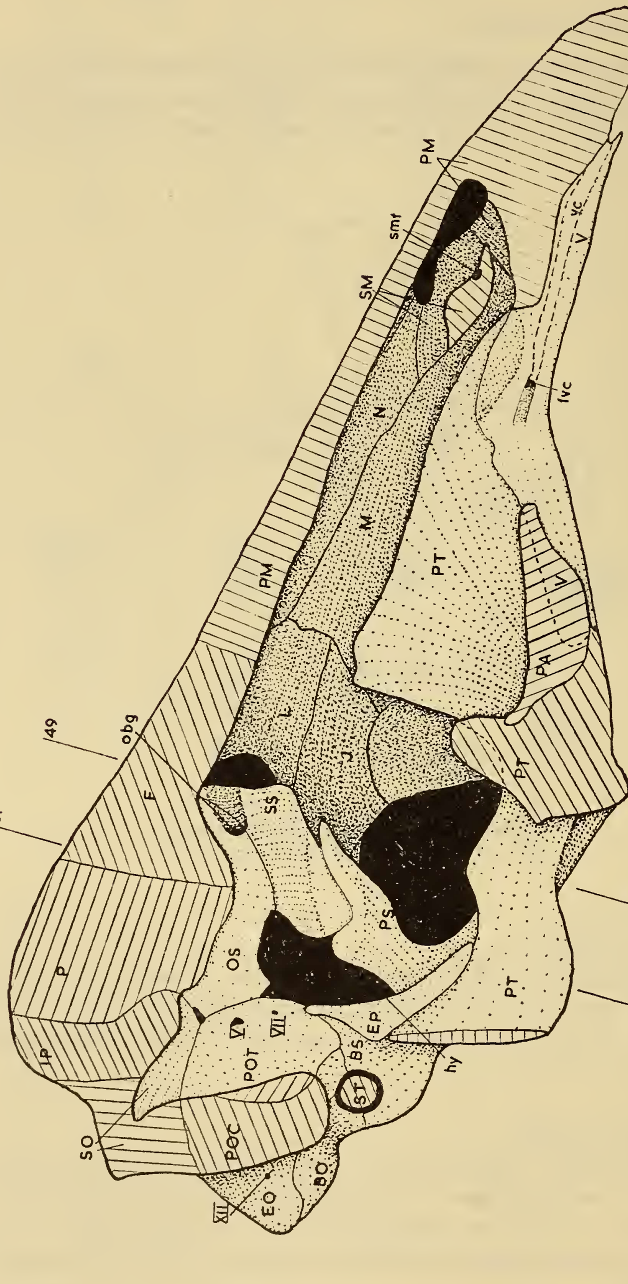


Fig. 45. *Jonkeria* sp. S.A.M. 11574 × ¼.
Parasagittal view of the skull drawn from a series of cross-sections.

In the snout there is a fairly well-developed septum formed by the pterygoids.

Lateral to the hypophyseal fenestra lies an epipterygoid of small dorsal extent.

The large hypophyseal fenestra, the moderately developed interorbital septum, the posteriorly truncated pterygoidal septum and the weakly developed epipterygoid, all indicate that the skull is in all probability not fully mature.

The constituent bones of the lateral wall of the braincase are: exoccipital, supraoccipital, opisthotic, proötic, orbitosphenoid and septosphenoid.

The proötic is well developed; posteriorly firmly applied to the opisthotic, dorsally meeting the anteriorly directed flange of the supraoccipital, ventrally resting on the basisphenoid, anteriorly, its lower half has a free edge forming the posterior border of the hypophyseal fenestra, whereas its upper half abuts against the orbitosphenoid. Near its anterior edge there are two foramina; the upper is a relatively small trigeminal foramen and the lower the small foramen for the facialis (VII).

The orbitosphenoid is an elongated bone dorsally, applied to the under surface of the parietal and frontal; ventrally it has a free edge which forms the upper border of the large hypophyseal fenestra; antero-ventrally it rests on the septosphenoid along an oblique suture.

At the junction of orbitosphenoid, proötic and supraoccipital lies a slit-like foramen probably for the IVth nerve.

The septosphenoid presents a large lateral surface. Dorsally it meets the orbitosphenoid and the under surface of the frontal. Ventrally it rests on the parasphenoidal and presphenoidal median septum.

Dorso-anteriorly the outer face of the septosphenoid is hollowed out and in this groove the olfactory tract opens and in it lies the olfactory bulb. Behind the groove the septosphenoid meeting the orbitosphenoid forms the lateral wall of the olfactory tract. Below this level the septosphenoid forms a median septum which ventrally fits into a groove of the parasphenoid and ?presphenoid.

The parasphenoid indistinguishably fused with the presphenoid forms a rather weak median septum which is dorsally forked to receive the septosphenoid.

The median septum of the snout is mainly formed by the pterygoids but anteriorly it is flanked by weak septal flanges of the vomers.

The epipterygoid is weakly developed in this specimen which appears to be immature. The footplate is elongated and quite strong but the ascending columella is but feebly developed. In the mature skull the epipterygoid probably meets the parietal and would thus largely cover the fenestra laterally of the cavum epiptericum.

Sagittal view (Fig. 46)

It is apparent that the floor of the braincase is incompletely ossified. Dorso-anteriorly of the basioccipital the two proötics have not met in the median line

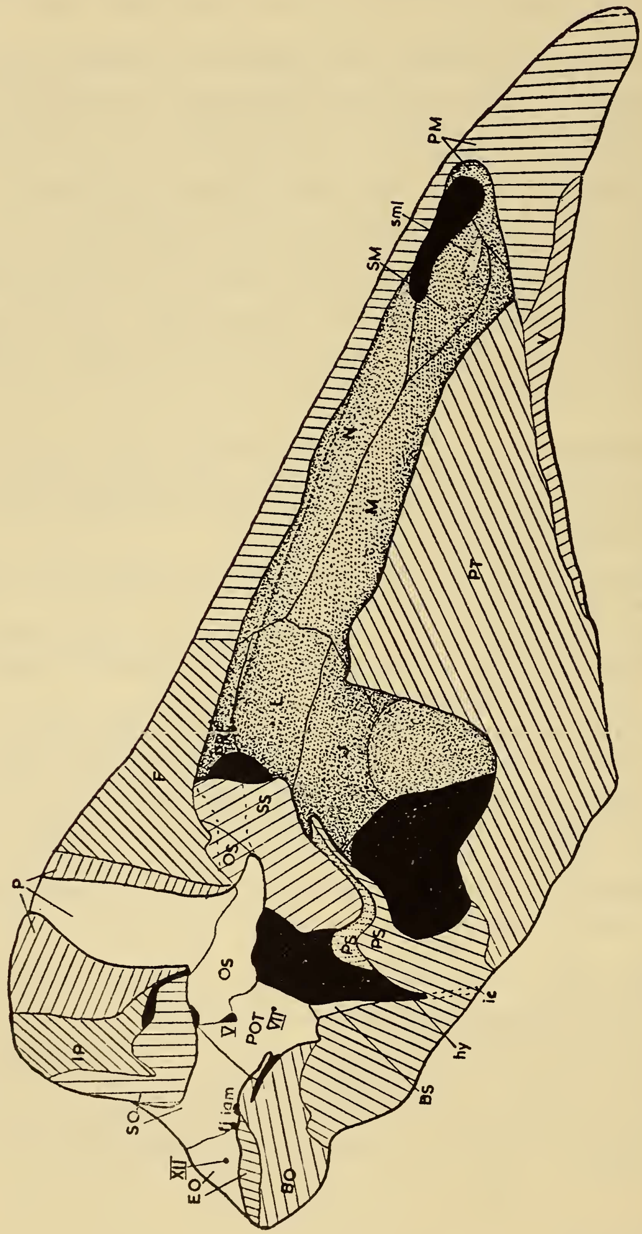


FIG. 46. *Jonkeria* sp. S.A.M. 11574 × ¼. Sagittal view drawn from cross-sections.

so that the upper part of the dorsum sellae is unossified.

The presphenoid cannot be identified as a separate element, but is probably represented by the weakly and incompletely ossified area lying postero-dorsally of the parasphenoidal septum.

The orbitosphenoid has its ventral part unossified. The exit of the optic nerve (II) is thus through the upper part of the large lateral fenestra.

The septosphenoid is seen to form a well-developed median septum which in its dorsal part separates the paired olfactory tracts and the olfactory bulbs.

The median septum of the snout is seen to be formed of an extensive vertical sheet formed by the pterygoids extending right up to the premaxilla

Cross-sections through the sphenoidal region (Fig. 47)

This series of sections, from front to back, show the relations of the orbito- and septosphenoids.

49. The septosphenoid is a simple median septum with a ridge indicating the ventral limit of the groove housing the olfactory bulb. Dorsally there is a pocket in the frontal and prefrontal for the posterior end of the nasal sac.
51. The olfactory groove becomes deeper and the tip of the parasphenoid is seen bifurcating.
53. The groove becomes pinched in before entering the tube for the olfactory tract.
54. The olfactory tracts lie in tubes enclosed above by the orbitosphenoids and below by the septosphenoid.
55. The pair of olfactory tracts coalesce to house the olfactory lobes in a kidney-shaped tube.
57. The parasphenoid diverging dorsally clasps the septosphenoidal septum.

59 & 61. Show the orbitosphenoids only forming the lateral walls and no longer roofing the cerebral hemispheres. The parasphenoid forms a thin septum.

The basicranial axis (Fig. 48)

The accompanying figure shows the basicranial axis and its relations to the adjacent bones.

The primitive basipterygoidal processes are not distinguishable. Their original situation is indicated by the sutural faces for the epipterygoid and pterygoid.

The parabasisphenoidal tubera are quite prominent and the outer borders of the fenestra ovalis is seen to be formed by the basioccipital, parabasisphenoid, proötic and opisthotic.

Two pairs of foramina pierce the parabasisphenoid, the posterior are the internal carotid foramina and the anterior pair the accessory carotid foramina.

The parasphenoidal rostrum is weak and is directed sharply upwards at an

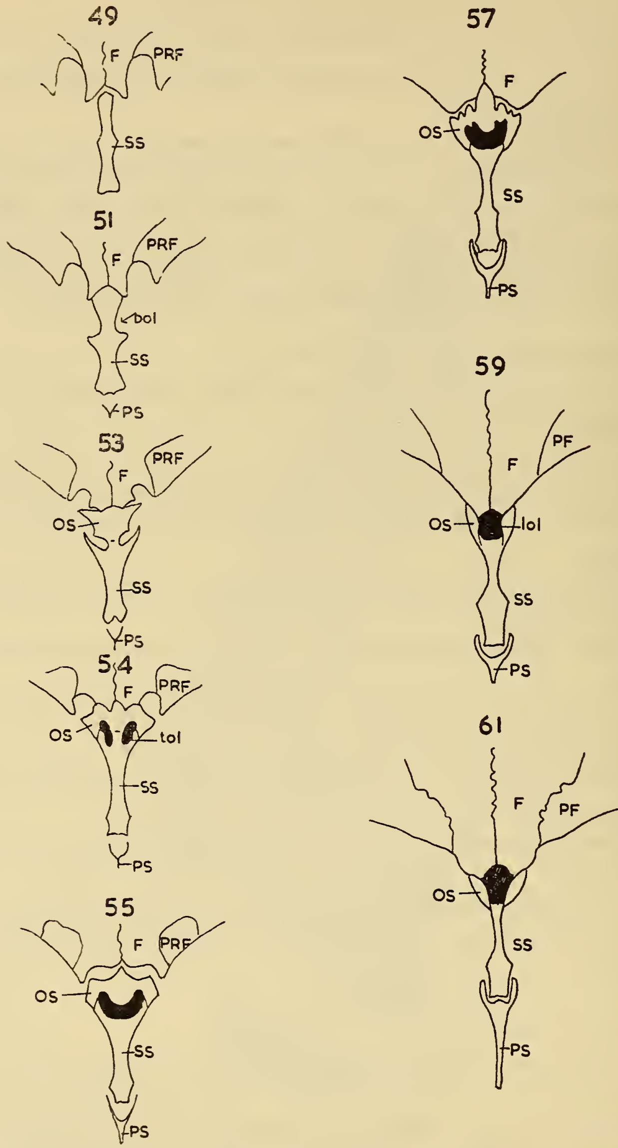


FIG. 47. *Jonkeria* sp. S.A.M. 15574 × ¼.
A series of sections, from front to back, through the sphenoidal region.

angle of about 100° to the lower edge of the axis.

The postero-dorsal bulge in the septum may be formed by a presphenoid.

The endocranial cavity (Fig. 49)

The incomplete ossification in the proötic and sphenoidal regions of the

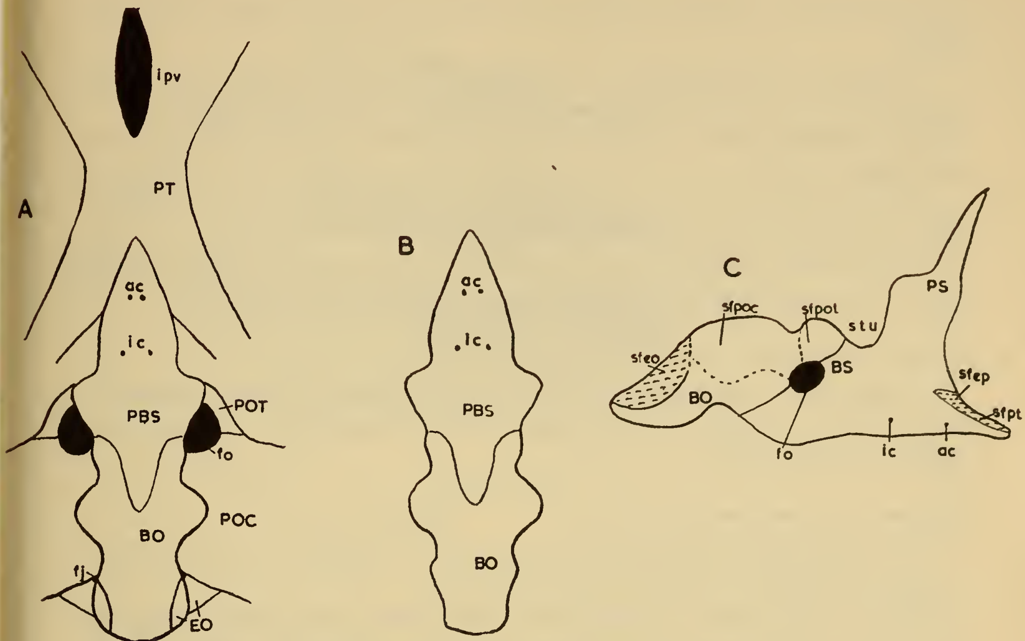


FIG. 48. *Jonkeria* sp. S.A.M. 11574 × ¼.
The basicranial axis reconstructed from serial cross-sections. A. Ventral view, with contiguous bones. B. Ventral view. C. Lateral view.

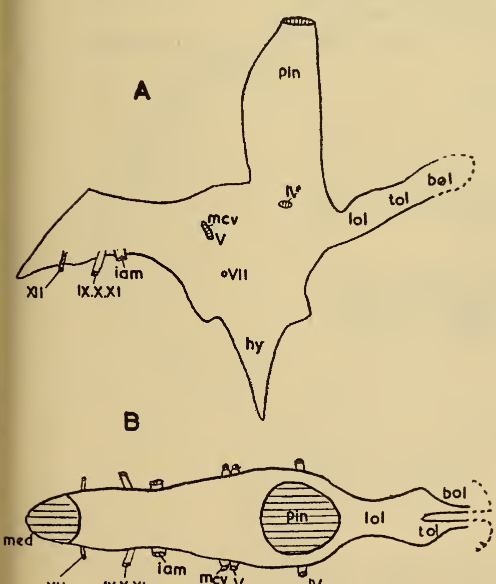


FIG. 49. *Jonkeria* sp. S.A.M. 11574 × ¼.
The endocranial cavity reconstructed from serial sections. A. Lateral view. B. Dorsal view.

endocranial floor prevents us from determining the lower border of the mid-brain.

The roots of the posterior cranial nerves lie near the ventral edge; the trigeminal exit lies well up the side and the IVth nerve emerged high up.

The olfactory lobes must have been very poorly developed. The tractus olfactorius was short.

The parietal canal is of moderate height—about 90 mm and the maximum antero-posterior and side to side diameter 40 mm.

The parietal foramen is much smaller than the diameters of the parietal tube, due to a forward growth of the upper part of the posterior wall.

S.A.M. 11575 *Jonkeria* sp.

I have cut a series of cross-sections of this specimen, which consisted of a snout found in association with S.A.M. 11574. From these I have prepared three graphic reconstructions.

The snout in parasagittal view (Fig. 50)

The interchoanal bar formed by the vomers is pierced by a pair of tunnels running through the vomers from back to front.

Each tunnel enters the bone from a longitudinal groove high up the side of the bar and has its exit between the anterior end of the vomer and the premaxilla. They housed a branch of the naso-palatine nerve.

Dorsally the vomer is pinched in and here forms a sheet of bone flanking the sagittal septum composed of the pterygoid. The pinched-in hollow in the vomer housed the lower part of the nasal capsule. Anterior to this lies the direct air passage (abnp) between external and internal nares.

In this figure the inner surface of the septomaxilla is shown. At the posterior

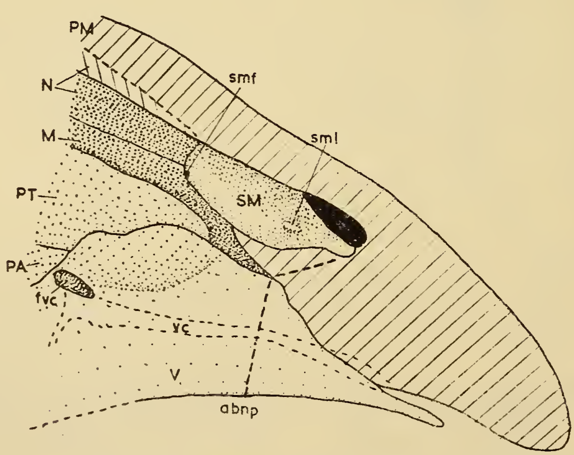


Fig. 50. *Jonkeria* sp. S.A.M. 11575 × ¼.
Parasagittal view of the snout reconstructed from sections.

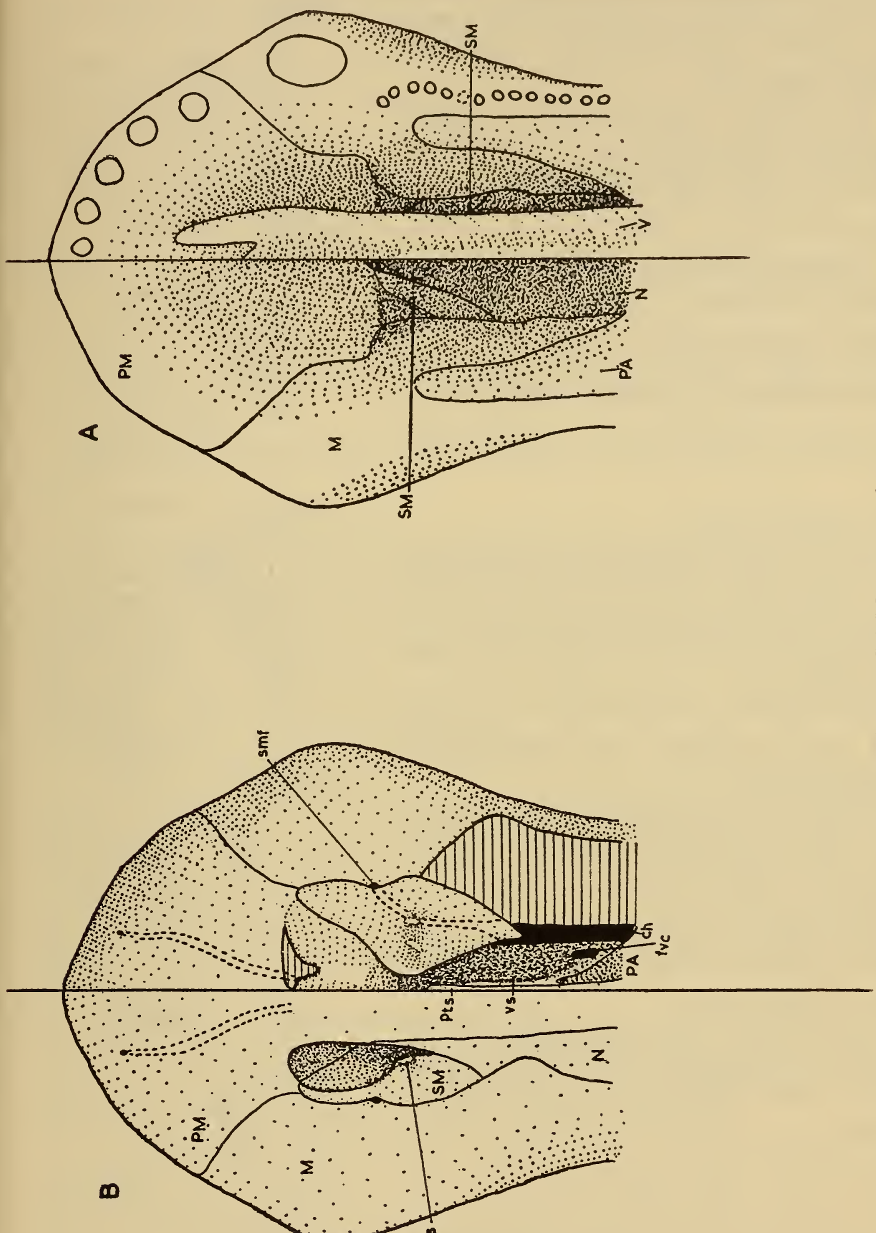


FIG. 51. *Jonkeria* sp. S.A.M. 11575 × ¼.
A. Ventral view of snout with right vomer removed. B. Dorsal view of snout with the roof-bones of the right half cut away.

edge of the septomaxilla lies the inner opening of the septomaxillary foramen. In its anterior half it carries a horizontal ledge which forms the floor of the naris.

The interior border of the air passage leading from the external naris to the choana is shown by a thick broken line (abnp).

Ventral view (Fig. 51)

A reconstructed ventral view shows the choanae in relation to the nares. From the anteriorly situated naris the direct air passage to the choana runs backwards below the horizontal ledge of the septomaxilla, whereas the passage to the olfactory sac runs above this ledge.

Dorsal view (Fig. 51B)

On the right side part of the premaxilla and maxilla and the whole nasal bone are shown cut away to expose the floor of the naris, the choana and the dorsal surface of the inter-choanal bar.

The anterior and lateral part of the floor of the nostril is formed by the premaxilla and the septomaxilla.

Medially lies the direct air passage passing below the ledge of the septomaxilla to the choana. The passage above the ledge leads to the olfactory sac.

The course of the septomaxillary tunnel from the internal to the external opening is shown in broken lines.

In the median line the median septum formed by the pterygoids and vomers is shown to form a partial wall between the two olfactory cavities.

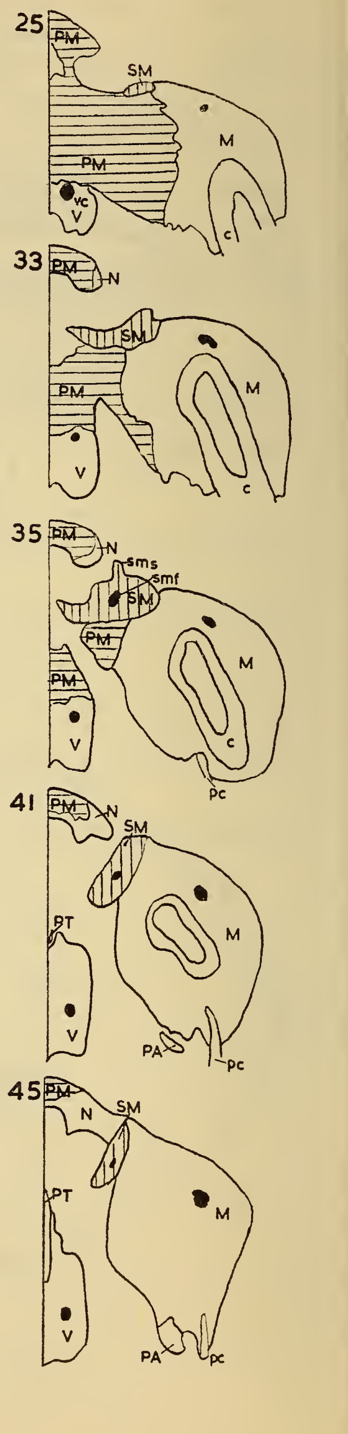


FIG. 52. *Jonkeria* sp. S.A.M. 11575 × ½. A series of sections from front to back, through the septomaxilla.

The foramen (fvc) leading into the longitudinal tunnel through the vomer lies lateral to the choana in the dorso-lateral surface of the vomer.

Sections (Fig. 52)

Five cross-sections are here reproduced to show the relations of the septomaxilla.

25. A section through the anterior part of the nostril which shows the nostril floor to be formed chiefly by the premaxilla. Note the forward extension of the nasal cavity into the premaxilla.
33. The septomaxilla now forms the outer part of the floor, whereas the premaxilla forms the median part of the floor over which passes the direct air passage to the choana.
35. The median and lower direct air passage is seen connecting with the choana; whereas the septomaxilla forms the floor for the higher olfactory passage.

41 & 45. Show the median septum formed by the pterygoids and vomers.

The Dinocephalian Braincase

From the foregoing detailed descriptions of the specimens studied it has become clear that the three groups of the Dinocephalia studied (unfortunately I have no suitable specimen of the Styracocephalia), viz. the Anteosauria, Tapinocephalia and the Titanosuchia, have much in common as far as the structures here examined are concerned. A general account for the Dinocephalia as a group can now be presented and this can be followed by a comparative consideration of the constituent sub-groups.

In lateral view very little of the ossifications of the original chondrocranium can be seen. Ventrally only the lower face of the basioccipital and of the exoccipitals and opisthotic are exposed—the rest being sheathed by the parasphenoid. Posteriorly the basioccipital, exoccipitals and the supraoccipital are seen enclosing the foramen magnum, with the opisthotic extending laterally to form the stout paroccipital process. Laterally the stout postorbital bar obscures most of the lateral face of the braincase and through the orbit little of the interorbital septum can be seen.

Dorsally of course the dermal bones of the roof overlie the endochondral bones. A parasagittal cut removes the lateral dermal bones and the bones of the palatoquadrate so that the braincase can be seen in lateral view with the opisthotic and supraoccipital showing a sectioned lateral face.

In contrast to their pelycosaur ancestors and also to all contemporary therapsids of the *Tapinocephalus* zone, the dinocephalian brain is well enclosed in a practically complete bony box of strongly ossified bones. Except for the openings for the cranial nerves, blood vessels and otic ducts (endo- and perilymphatic) there is one large lateral opening representing the original metoptic fissure situated between the pila antotica and the pila metoptica. Anteriorly the nasal capsule is of course unossified so that the bulbus olfactorius is not covered laterally by bone.

The closure of the lateral wall above the pituitary fossa is effected by the meeting of the ossifications of the otic and sphenoidal regions. This is in part due to the posterior location of the sphenoidal ossifications, but also to the well-developed condition of the otic ossifications which have extended well forwards. The proötic and supraoccipital both extend well anterior to the plane of the original proötic incisure.

The bones enclosing the brain are: the exoccipitals, basioccipital, basisphenoid, supraoccipital, opisthotics, proötics and the sphenoids with the parasphenoid sheathing the basisphenoid ventrally and the sphenoid complex clasped and supported ventrally by the presphenoid and the parasphenoidal rostrum.

The exoccipital

In posterior view the exoccipitals form the upper and latero-dorsal part of the stout condyle. Laterally they overlap on to the posterior face of the opisthotic and dorsally on to the posterior face of the supraoccipital.

The two exoccipitals meet each other in the median line and thus form the surface on which the medulla and hindbrain rest. The exoccipital part of the floor ends just posterior to the plane in which the internal auditory meati lie. Anterior to this lies a hump formed by the basioccipital. Laterally each exoccipital curves upwards to form most of the lateral rim of the foramen magnum. Dorsally it meets the supraoccipital and thus forms the lower posterior part of the sidewall. The inner face of the exoccipital is pierced by two foramina situated low down on the sidewall, practically at floor level. The smaller and posterior foramen gives exit to the hypoglossal nerve (XII). The larger and anterior foramen, the so-called jugular or vagus foramen, forms the inner opening of a long tube (25 mm in length in a specimen of *Struthiocephalus*) which in addition to nutritive vessels housed the glossophargeal (IX), vagus (X) and the accessory (XI) nerves. The exoccipital is really notched not pierced by this foramen as it forms only the posterior half of the border—the anterior half being formed by the opisthotic. In some cases these two tubes merge and open into a single external foramen.

The basioccipital

The basioccipital forms the ventral part of the condyle. Posteriorly a notochordal pit is evident. This unossified part sometimes extends anteriorly under the exoccipitals and may even join an unossified space lying between the basioccipital and the proötic.

Ventrally the basioccipital overlaps the lower face of the opisthotic, where it is notched to form the inner edge of the jugular foramen.

The basioccipital makes only a very small contribution to the floor of the braincase. Just posterior to the plane in which the internal auditory meati lie, the ends of the exoccipitals diverge and here there lies a low hump in the floor composed of basioccipital. Anterior to the vestibules the basioccipital meets the proötics above in an unossified zone.

Anteriorly the basioccipital abuts against the basisphenoid and internally forms part of the inner face of the foramen ovale.

The proötics

In lateral and anterior views the proötic is seen to have an extensive outer face as it lies firmly ankylosed against the inner face of that part of the occipital plate formed by the supraoccipital and the opisthotic and its paroccipital process. Anteriorly an edge of the proötic forms the posterior border of a large fenestra—the trigeminal foramen. This is in some cases transformed to two separate openings—the upper one for the median cerebral vein and the lower for the trigeminal nerve. Anterior to the fenestra a pillar of the proötic ascends and this in some cases meets a descending pillar of the supraoccipital to enclose the trigeminal fenestra anteriorly.

The two proötics meet each other in the median line to form the floor of the braincase anterior to the plane in which the internal auditory meati lie. The proötics form a transverse ridge across the brain floor and the anterior face of this ridge forms the upper part of the dorsum sellae. The lower part of the posterior wall of the sella turcica is formed by the basisphenoid. Laterally, just behind the transverse proötic ridge, the proötic forms the anterior border of the internal auditory meatus, whose posterior border appears to be formed by the opisthotic. From the floor the proötic laterally curves upwards to form part of the side wall, where it posteriorly and dorsally meets the downwardly extending inner face of the supraoccipital.

The most lateral anterior edge of the proötic forms the posterior border of the large trigeminal fenestra. More medially and anteriorly the proötic forms a dorsally directed stout process developed in the pila antotica and this pillar forms the lower half of the anterior border of the trigeminal fenestra. Here it often meets the downwardly directed process of the supraoccipital. The original proötic incisure is thus closed anteriorly and a proötic fenestra is thus formed and this is directed much anteriorly.

The median ventral face of the proötic abuts against the ascending process of the basisphenoid and these two together form the dorsum sellae. Higher up the anterior edge of the proötic meets the orbitosphenoid.

Just behind this edge and below the trigeminal fenestra the proötic is pierced by a foramen for the facial nerve (VII).

The supraoccipital

In the internal face of the braincase the supraoccipital forms the upper smaller part of the lateral rim of the foramen magnum above the exoccipital. Extending dorsally it forms the dorsal edge of the foramen magnum and from here anteriorly it forms the whole domed roof of the brain up to the root of the parietal organ.

In the lateral wall the supraoccipital descends to meet the anterior edge of the exoccipital and the dorso-posterior edge of the proötic and the opisthotic.

Anterior to the plane in which the trigeminal fenestra lies, a process of the supraoccipital descends to meet the ascending proötic process formed in the pila antotica to form the upper part of the anterior border of the trigeminal fenestra. The anterior edge of this process meets the posterior edge of the orbito-sphenoid. Antero-dorsally the supraoccipital meets the parietal where the parietal organ emerges from the brain.

Postero-dorsally of the internal auditory meatus is an outward directed bulge for the flocculus.

The basisphenoid

The basisphenoid houses the pituitary fossa of which it forms the anterior and most of the posterior face. At the bottom of the pit a pair of foramina enter carrying the internal carotids. No demarcation between the basisphenoid and the sheathing parasphenoid is usually evident, cf. *Jonkeria.*

There being no sidewalls to the sella turcica the metoptic fissure is patent and the pituitary vein has no special foramen but it would appear that both the oculomotorius (III) and the trochlearis (IV) emerging higher up pierce the posterior part of the sphenethmoid complex.

The opisthotic

In its median part the opisthotic is firmly ankylosed to the supraoccipital above and the proötic anteriorly. Laterally it is produced as a very strong paroccipital process and forms most of the rim of the foramen ovale—posteriorly, anteriorly and laterally.

In the inner face of the endocranial cavity the opisthotic has no great face and appears only to enter into the rim of the internal auditory meatus. Lateral to this it of course houses the internal ear.

The parietal

Above and between the foramina for the exit of the pair of trochlear nerves the braincase has a large dorsal foramen whose rim is wholly formed by the parietals. This is the lower end of the parietal tube which pierces the greatly thickened skull roof.

Laterally the ventral edge of the parietals rest on the upper edges of the supraoccipital and the sphenoid complex. Here the parietal tube is somewhat constricted—but immediately widens again with a decided posterior bulge—then narrows again with the tube during the whole length presenting in section an irregular oval outline. Dorsally at its opening on to the outer surface the tube is again somewhat constricted and the outer parietal or pineal foramen usually opens in the middle of a mound.

The parietal tube varies in length from 100–320 mm. Its walls are smooth and formed of compact bony tissue.

The sphenoidal region

Anterior to the otic region lies the sphenoidal complex usually in maturity well ossified. Ventrally it rests in the form of a median septum on the septum formed by the parasphenoid. Dorsally it is intercalated between the frontals. Posteriorly it meets the parietal, supraoccipital and proötic, but postero-ventrally the sidewall is fenestrated as here the metoptic fissure is still patent and the hypophysis laterally not enclosed with bone.

The sphenoidal complex is composite and the limits of the component parts difficult to determine as the sutures are in maturity usually closed, but from the sections it is manifest that three discrete elements are present, viz. a presphenoid, an orbitosphenoid and a septosphenoid.

The presphenoid is a sheet of bone lying in the median plane and ventrally resting on the parasphenoidal septum to which it is usually intimately fused, and dorsally supports the septum formed by the septosphenoid. Its posterior edge forms the anterior border of the pituitary fossa.

The septosphenoid is also a vertically orientated sheet of bone which rests ventrally on the upper edges of the presphenoid and the parasphenoid. Its posterior edge is free and forms the upper part of the anterior border of the hypophysal fenestra. Dorsally it is clasped by the frontals.

In its dorso-anterior part a pair of lateral grooves are developed separated by a median septum. The posterior part of the olfactory bulbs are housed in these grooves. The olfactory bulbs thus have no lateral bony wall. Posterior to these grooves the olfactory tracts are housed in a pair of tubes.

The orbitosphenoids form the postero-dorsal part of the sphenoidal complex. They form the postero-dorsal part of the median septum. From this median stem the pair of orbitosphenoids curve round the thalamus and the cerebral hemispheres. Just above the median stem each orbitosphenoid is pierced by a large rounded foramen for the optic nerve (II).

Dorsally the orbitosphenoids abut against the under surface of the parietals and frontals and under the frontals the two orbitosphenoids meet each other in the median line to form a roof for the cerebral hemispheres.

Posteriorly each orbitosphenoid meets the supraoccipital high up in the sidewall and lower down the proötic to form a bony lateral wall enclosing the brain.

The ethmoidal region

Anterior to the sphenoidal region there are in the Dinocephalia no ossifications in the ethmoidal region nor in the nasal capsules.

Anterior to the parasphenoid the median septum is formed by a high sheet of the pterygoids flanked by upgrowths of the vomers.

Contemporary therapsids

In order to enable me to compare the nature of the braincase, basicranial axis and median septum in the Dinocephalia to that developed in their contemporary fellow therapsids I present here descriptions of these structures as determined in one specimen of a dicynodont and in two pristerognathid therocephalians. Unfortunately I have as yet not been able to collect a suitable specimen of a gorgonopsian.

(*a*) DICYNODONTIA

S.A.M. 12217 *Dicynodon* sp.

I have cut a series of 62 cross-sections of a fair-sized *Dicynodon* skull from the lower part of the *Tapinocephalus* zone.

For comparison with the foregoing Dinocephalia I have graphically reconstructed views of the skull in the same way as for the Dinocephalia.

Parasagittal view (Fig. 53A)

The braincase occupies a great part of the length of the skull—74% (*Moschops* 59%, *Struthiocephalus* 44%, *Jonkeria* 34%, *Anteosaurus* 32%) and also of the height of the skull (excluding the thickness of the roof-bones) viz. 61% (*Moschops* 41%, *Struthiocephalus* 41%, *Anteosaurus* 40%, *Jonkeria* 36%). The braincase is high relative to its length—79% (*Anteosaurus* 31%, *Moschops* 26%, *Struthiocephalus* 25% and *Jonkeria* 21%).

But its sides are widely open. There is a large gap between the sphenoidal region and the otic region.

The anterior extent of the proötic is not great and the trigeminal emerges through a notch at the junction of the proötic and the supraoccipital.

The sphenoidal complex situated far forward is very well developed. Dorsally it is applied to and intercalated between the frontals. Its median septal part extends far ventrally where it rests on the tip of the parasphenoidal rostrum.

On its dorso-anterior face there is a groove which housed the olfactory bulbs. Posteriorly this groove pierces the bone and connects with the trough which houses the unpaired olfactory lobes.

The sides of this trough may be formed by a separate bone. A notch posteriorly indicates its limits.

The complex would then be composed of a median septal part—the septosphenoid—and a pair of wings—the frontosphenoid or orbitosphenoid.

The parasphenoidal rostrum, which lies horizontally stretches far forward to make contact with the palatal sheets of the premaxillae. On its dorsal edge it carries a sheet of bone directed antero-dorsally towards the postero-ventral edge of the septosphenoid. This is the presphenoid.

Anteriorly the lower edge of the parasphenoidal rostrum rests on the upper surface of the vomers, which lie far posteriorly in the middle third of the skull. The choanae lie posterior to the anterior third of the skull.

Anterior to the vomers the premaxillae form a well-developed median septum in the snout.

The fenestra ovalis pierces the basioccipital well above the lower edge, here formed by the strong basioccipital tubera.

The epipterygoid has a fairly short footplate resting on the pterygoid and meeting the basisphenoid at the basipterygoidal process. Its ascending process which is fairly slender is directed somewhat anteriorly and meets the under surface of the parietal.

The quadrate ramus of the pterygoid is low and weak.

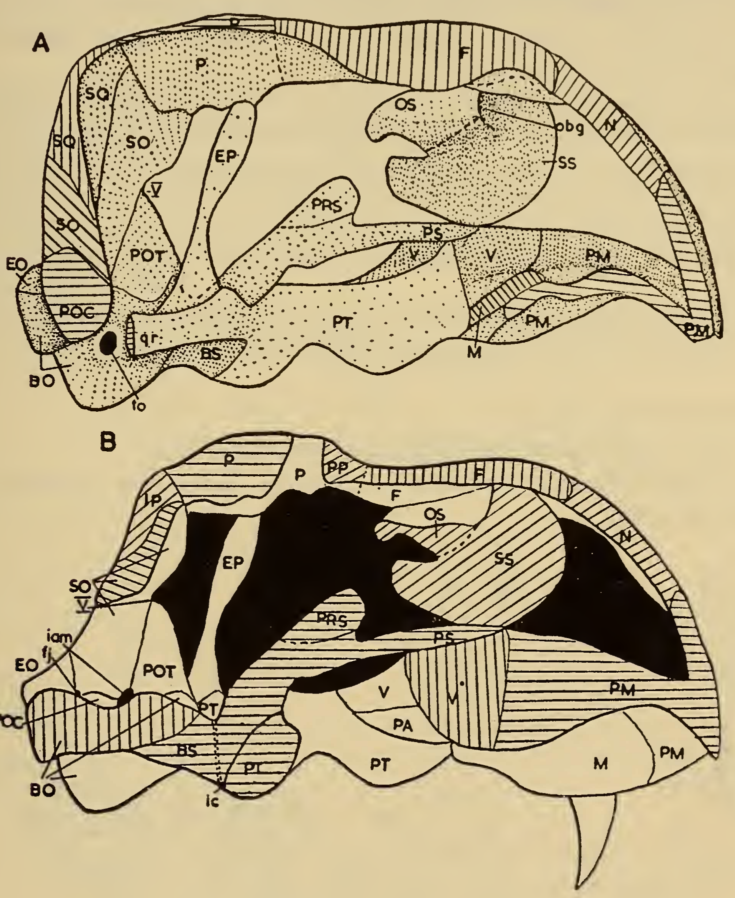


FIG. 53. *Dicynodon* sp. S.A.M. 12217 × 1.
A. Parasagittal view of the skull as reconstructed graphically from a series of cross-sections. B. Sagittal view.

Sagittal view (Fig. 53B)

The posterior part of the braincase is seen to have its lateral wall formed by the exoccipital, supraoccipital, opisthotic and proötic; the floor is formed by the basioccipital which is anteriorly not overlain by the proötics. The proötics fail to meet each other in the middle line so that the upper part of the sella turcica has no ossified dorsum. The lower part of the dorsum sellae is as usual formed by the basisphenoid. The sella turcica also has only a short ossified frons formed by the basisphenoid. The hypophysis was thus apparently small.

The jugular foramen and internal auditory meatus lie at floor level, but the notch for the exit of the trigeminal nerve lies very high in the sidewall. The roof is formed by the supraoccipital and parietal. There is also a downwardly directed flange of the parietal into the sidewall.

The large middle part of the braincase wall is unossified, but in a more lateral plane lies the slender epipterygoid. The floor is here formed by the basisphenoid and presphenoid.

In the sphenoidal region the sidewall is formed by flanges of the frontal meeting the curved wings of the orbitosphenoid, which also forms the floor for the olfactory tract. Further anteriorly the median septum of the septosphenoid separates the grooves housing the paired olfactory bulbs. The parasphenoidal rostrum lying horizontally is seen to overlie the vomers which lying far back form a deep median keel. Anteriorly the premaxillae carry a fairly high dorsal septum.

Anteriorly the pterygoids do not enter the median plane and neither do they develop any dorsal parasagittal septa.

The basicranial axis (Fig. 54)

I have reconstructed three figures of the cranial base.

In A the basicranial structures are shown in ventral view in relation to the contiguous bones.

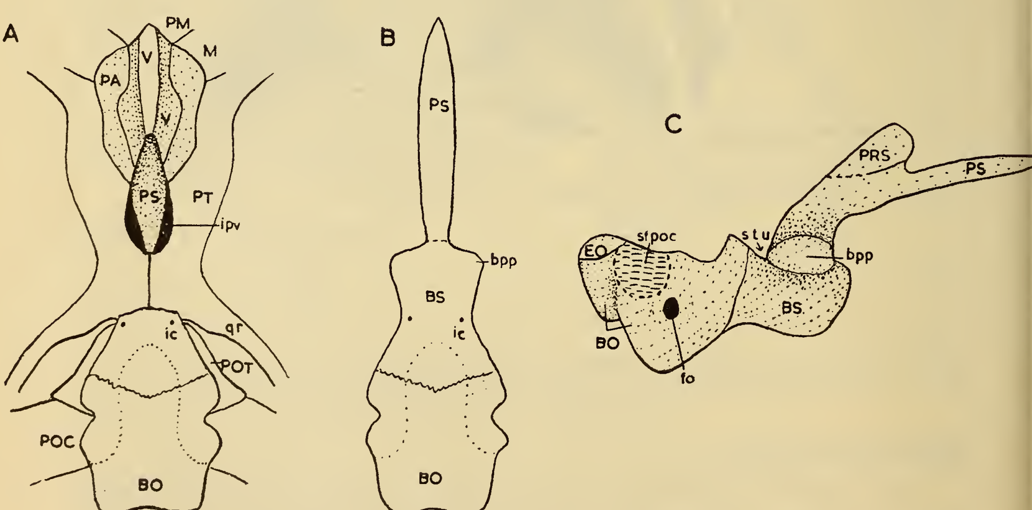


Fig. 54. *Dicynodon* sp. S.A.M. 12217 × 1
Basicranial axis reconstructed from serial sections. A. Ventral view in relation to the surrounding bones. B. Ventral view. C. Lateral view.

The parasphenoidal rostrum is seen lying above the interpterygoid vacuity with its anterior end underlain by the vomers, which here carry a well-developed ventral keel.

The choanae are seen to open posteriorly to the edge of the premaxilla into longitudinal grooves roofed by the vomers and flanked by the palatines.

In B the adjacent bones have been removed to show the basicranial bones in ventral view. The basipterygoidal processes are still quite prominent. In C the above is seen from the side and the dorsum sellae appears to have its upper part formed by the basioccipital.

The endocranial cavity (Fig. 55)

In the accompanying figures the endocranial cavity is shown in outline in lateral and dorsal view.

The brain cavity is long; wide and high posteriorly and low and narrow elsewhere.

The parietal tube is short (6 mm) and its diameters small (4·5 mm) and the sella turcica shallow.

The mes- and metencephala could have been well developed but the fore-brain could have had but a small volume.

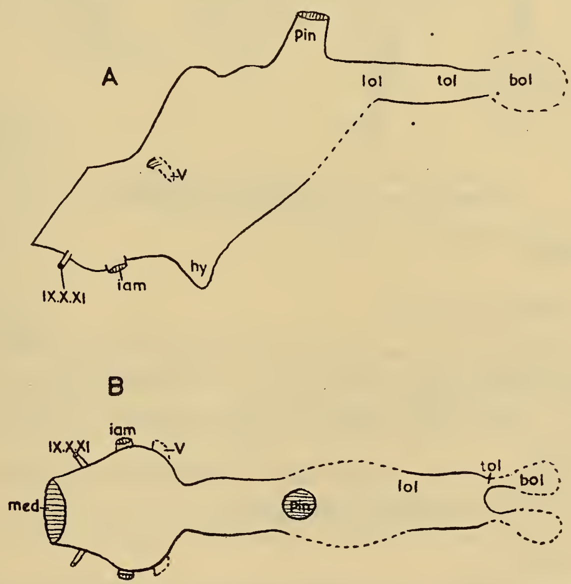


FIG. 55. *Dicynodon* sp. S.A.M. 12217 × 1.
The endocranial cavity reconstructed in outline from sections.
A. Lateral view. B. Dorsal view.

Sections (Fig. 56)

I am reproducing here four sections from front to back to show the structure of the sphenoidal region.

16. The septosphenoid forms a thin median septum and the median premaxillary septum is flanked by the anterior ends of the paired vomerine septum.
20. The sides of the septosphenoid are excavated for the olfactory bulbs. The posterior end of the premaxillary septum is clasped by the vomers. The tip of the parasphenoidal rostrum rests on the vomers.
24. The olfactory lobes are housed by the orbitosphenoids resting on a septum formed by the septosphenoid. The parasphenoidal rostrum is clasped by the vomers.
28. The orbitosphenoids lose contact with the median septum and the parasphenoidal rostrum rests on the vomers.

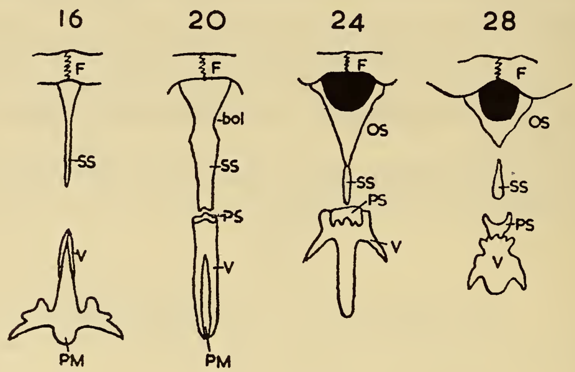


Fig. 56. *Dicynodon* sp. S.A.M. 12217 × 1.
Cross-sections through the sphenoidal region.

(*b*) THEROCEPHALIA

S.A.M. K210 *Maraisaurus parvus*

I have cut 82 cross-sections through the skull of this small pristerognathid from low down in the *Tapinocephalus* zone. From these I have reconstructed drawings on the same basis as for all the preceding specimens to facilitate direct comparisons.

Unfortunately, however, the sphenoidal region was unossified which leads one to conclude that the skull was immature.

Parasagittal view (Fig. 57)

In the posterior part the lateral wall of the braincase is formed by the exoccipital, paroccipital, supraoccipital and proötic.

The proötic has a large outer face. Its anterior edge is notched for the trigeminal nerve and above this there is a gap between the proötic and the supraoccipital. This lack of ossification also denotes that we are dealing with an immature skull.

The anterior part of the proötic is pierced by two small foramina for the VIth and VIIth cranial nerves.

The fenestra ovalis is bounded by the opisthotic, basioccipital, basisphenoid and proötic and is situated quite high up in the skull.

The epipterygoid has a long footplate and a fairly broad ascending columella.

It lies lateral to the sella turcica and to the anterior edges of the proötic and supraoccipital and meets the parietal.

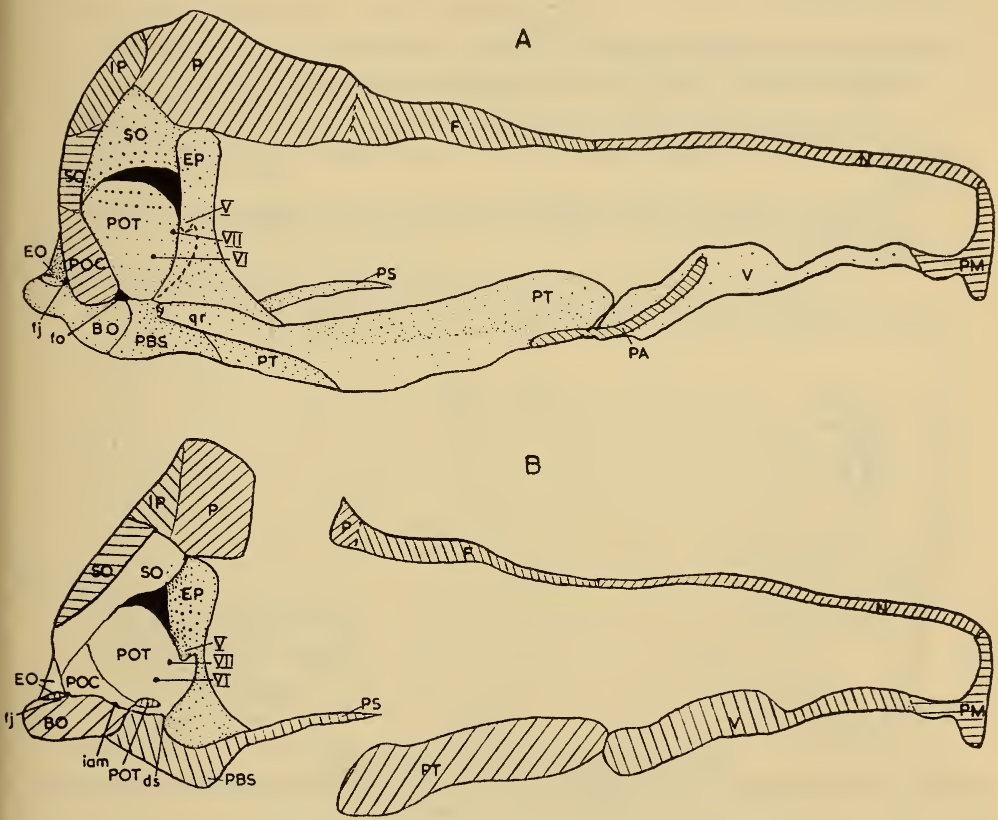


Fig. 57. *Maraisaurus parvus* S.A.M. K210 × 1.
A. Parasagittal view reconstructed from serial sections. B. Sagittal view.

The pterygoid dorsally bears a low septum. Posteriorly, above the inter-pterygoid vacuity, the paired parasagitally situated septa enclose a trough, but anteriorly these meet in the median line to form a single median septum. For a short distance the upper edge of this septum is forked and these would apparently clasp the lower edge of the septosphenoid when ossified.

Anteriorly the pterygoids do not extend in between the vomers.

Sagittal view (Fig. 57B)

The exoccipital forms the posterior part of the braincase floor. Most of the floor is formed by the basioccipital. Anterior to this the two proötics meet in the middle line above the basisphenoids with an unossified gap between them.

The upper part of the dorsum sella is thus formed by the proötics and the lower part by the basisphenoid.

The sella turcica is shallow with no frons.

The parasphenoidal rostrum lies horizontally and no presphenoid is ossified above it.

The basicranial axis (Fig. 58)

Three reconstructed views of the bones of the basicranium are given.

In A a ventral view shows the basal bones in relation to the supporting bones, with the parasphenoidal rostrum lying above the interpterygoidal vacuity.

In B the contiguous bones have been removed. The basispterygoid process is just evident.

In C a lateral view shows the horizontal disposition of the parasphenoidal rostrum, and the shallow sella turcica without an ossified frons.

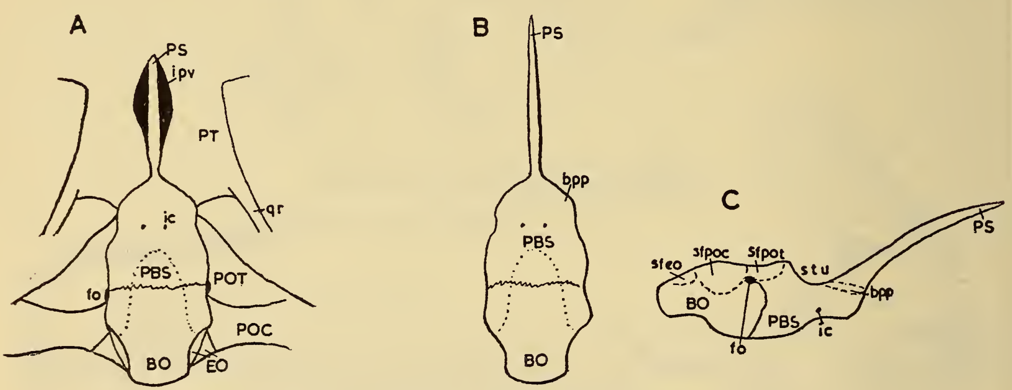


Fig. 58. *Maraisaurus parvus* S.A.M. K210 × 1.
Basicranial axis as reconstructed from serial sections. A. Ventral view in relation to contiguous bones. B. Ventral view. C. Lateral view.

Comparative

In a recent publication I attempted to show how the families of the therapsids diverged in pre-*Tapinocephalus* zone times, basing my views on the effects of the differential developments of the jaw mechanism.

Here I found that, as far as the South African therapsids were concerned, from a first divergence emerged the two suborders Anomodontia and Theriodontia. Two later splits produced from the former the two infra-orders Dicynodontia and Dinocephalia and from the latter the two infra-orders Gorgonopsia and Therocephalia.

To what conclusions does the above study of the braincase, basicranial axis and median septum bring us?

A review of the nature of these structures in the morphological series—primitive labyrinthodonts—captorhinomorphs to sphenacodont pelycosaurs may help to indicate the developmental trends towards the pre-*Tapinocephalus* zone eotherapsids and their immediate descendants.

The primitive labyrinthodonts (*e.g.* Palaeogyrinus)

In these forms in the sagittal plane, the occiput makes an angle of 90° with the basicranial axis (and the general level of the paalte and alveolar border of the upper jaw).

The long parasphenoidal rostrum thus lies horizontally and there is no downturn of the face.

The sphenethmoid resting on the parasphenoid and stretching dorsally to the frontals houses the anterior part of the brain which thus with the olfactory bulbs as a whole lies horizontally.

The exoccipital does not enter the brainfloor.

The sidewall of the braincase is well ossified with the exception of the ethmoidal region and nasal capsules.

The proötic is well developed, extending well forward to enclose the foramen for the Vth nerve, but it does not meet the sphenoidal bones above the metoptic fenestra. Below this fenestra the basisphenoid is intercalated between the proötic and the sphenethmoid and forms the floor of the shallow *sella turcica*, whose *dorsum* is formed by the proötic and the *frons* by the sphenethmoid.

In the sphenoidal region there is a single bone pierced by the foramen for the IInd nerve. The bone has two dorsal wings standing on a median septum, which is supported below on the parasphenoidal rostrum, which is long and lies horizontally. The bone does not form a roof for the braincase.

Both the *fenestra ovalis* and the *sella turcica* lie high up in the skull.

In the median line the ventral surface of the cranial base, formed by the basioccipital and the long parasphenoid, lies horizontally with the rostrum exposed through the long widely open interpterygoidal vacuity. Anteriorly the long processes of the pterygoids meet in the median line, but form no dorsal septum. Further anteriorly lie the short vomers in the same plane. There is no median dorsal septum in the ethmoidal region.

The captorhinomorphs

The occiput is slightly inclined forwards to make an angle of about 80° with the cranial base. The shortened parasphenoidal rostrum is slightly inclined upwards to make an angle of about 30° with the cranial base.

The sphenethmoid resting on the dorsally inclined parasphenoid houses the rhinencephalon, which is thus carried upwards away from a horizontal plane. The exoccipital does not enter the brainfloor.

The sidewall of the braincase is poorly ossified with a wide gap between the otic and sphenethmoidal regions.

The proötic is poorly developed, not extending forwards to enclose a foramen for the Vth nerve. It does not meet the sphenoidal bones. Below the metoptic fenestra it meets the basisphenoid, which forms the floor of the deep *sella turcica* and the very high *dorsum sellae.*

The single sphenethmoidal ossification is Y-shaped in section with the stem forming an interorbital septum.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the shortened upturned parasphenoidal rostrum is exposed through the long widely open interpterygoidal vacuity. Anteriorly the long anterior processes of the pterygoids meet in the median line but form no dorsal septum. Further anteriorly lie the elongated vomers in the same plane.

The pelycosaurs

In *Dimetrodon* the occiput is inclined further forwards to make an angle of about 60° with the cranial base.

The long parasphenoidal rostrum is inclined upwards with its tip lying on the upper edge of the high pterygoidal septum, well posterior to the vomer. There is thus a strong downturn of the face. The exoccipital forms the posterior part of the brainfloor.

The sidewall of the braincase is poorly ossified with a wide gap between the otic and sphenoidal regions.

The proötic is weakly developed; it does not extend far anteriorly and does not enclose a foramen for the Vth nerve; it does not meet the sphenoidal complex above the pituitary fenestra. Ventrally the two proötics meet in the middle line to form a high *dorsum sellae* of a fairly deep *sella turcica* whose *frons* as well as its floor is formed by the basisphenoid.

A median ossification is present in the interorbital region; it is essentially a vertical plate lying in the midline of the skull and split above so that it is Y-shaped in section. Its ventral septal part is clasped by the parasphenoid; its dorsal part encloses a tube in its posterior part, which is anteriorly divided into two for the olfactory tracts. It seems probable that this ossification is tripartite: the septal part being a septosphenoid and the wings orbitosphenoids with a foramen for the passage of the IInd nerve.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the long parasphenoidal rostrum is exposed through the fairly long and widely open interpterygoidal vacuity.

Anteriorly the very long anterior pterygoidal processes meet in the median line and form a high median dorsal septum. Further anteriorly the long vomers lie with their medio-ventral edges in nearly the same plane as the pterygoids. The vomerine septum is fairly low.

The early therapsids of the Tapinocephalus *zone*

The study of the structural features used in the above comparisons in the case of the early therapsids reveals such a great degree of variation that it is difficult to treat the infra-orders together as a group representing a single morphological stage beyond the pelycosaur stage.

Intermediate stages appear imperative in order to link up the pelycosaur and therapsid stages of development.

I will thus treat the 4 infra-orders separately and then indicate what intermediate proto-Therapsid stages could be postulated.

The Dinocephalia

In the three families Anteosauridae, Titanosuchidae and Tapinocephalidae the occiput is inclined *backwards* at an angle of 110°–170° to the cranial base. The median ventral edge of the fairly short parasphenoidal rostrum is inclined upwards to make an angle with the cranial base varying from 5° to 80°. There is thus little to very great downturn of the face. The parasphenoid meets or does not meet the high pterygoid septum and always ends far posterior to the vomer.

The exoccipital forms the posterior part of the brainfloor.

The sidewall of the braincase is always well ossified and the small fenestra between the otic and sphenoidal regions is dorsally closed through the meeting of the sphenoidal, otic and occipital bones. The braincase, however, lies far posteriorly with a large area between the sphenoidal region and the nostril without bony sides

The proötic is well developed, extending anteriorly and, together with a flange from the supraoccipital, meets the orbitosphenoid to close the dorsal part of the metoptic fenestra. The Vth nerve thus passes through a foramen enclosed by bone. Ventrally the two proötics meet in the median line and thus form the upper part of the *dorsum sellae.* The *sella turcica* is very deep with the lower part of the *dorsum sellae* and the floor formed by the basisphenoid. The *frons* is formed by the presphenoid which forms a vertical septum standing on the parasphenoid.

In the interorbital region there is a well-ossified sphenoidal complex consisting of a median septum formed by a septosphenoid resting on the para- and presphenoid. Above the septosphenoid the orbitosphenoids, pierced by a foramen for the IInd nerve, form wings posteriorly enclosing a single tube for the olfactory lobes and anteriorly a pair of tubes for the olfactory tracts.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the short parasphenoidal rostrum is mostly invisible in palatal view through the reduction of the length and width of the interpterygoidal vacuity.

Anteriorly the anterior pterygoidal processes meet in the median line and form a very high and long dorsal septum extending anteriorly in between dorsal flanges of the vomers.

Further anteriorly the vomers, with strong dorsal septa, are inclined upwards at an angle of 5°–40° to the cranial base.

The Dicynodontia

In a *Dicynodon* from the *Tapinocephalus* zone the occiput is inclined forwards at an angle of 80° to the cranial base.

The long parasphenoidal rostrum is inclined upwards at an angle of 25° to the cranial base.

There is thus considerable downturning of the face.

The parasphenoid anteriorly rests on the vomer since the pterygoids do not meet in the median line anterior to the interpterygoidal vacuity.

The exoccipital does not form the posterior part of the brainfloor.

The sidewall of the braincase is widely open, due to the poor development of the proötic and the extreme forward position of the sphenoidal complex. The brain is thus very long in relation to the total skull length.

The proötic is weakly developed and does not even extend so far anteriorly as to form a notch for the Vth nerve. Ventrally the two proötics do not meet in the median line and have no part in the formation of a *dorsum sellae*, this being formed by basisphenoid and basioccipital.

The *sella turcica* is shallow, with its *frons* formed by the parasphenoid.

The presphenoid is a vertical sheet of bone in the median line standing on the parasphenoidal rostrum and it makes no contact with the anteriorly situated interorbital sphendoidal complex.

The sphenoidal complex is well ossified and consists of a ventral septal sheet resting on anterior tip of the parasphenoidal rostrum. This is the septosphenoid. Above rests two wings enclosing the forebrain. These are the orbitosphenoids. A posterior notch serves for the passage of the IInd nerve.

The *fenestra ovalis* appears to lie high up in the skull but this is due to the development of the strong basioccipital tubera.

In the median line the long parasphenoidal rostrum is well exposed through the long and wide interpterygoidal vacuity.

With the radical change in the nature of the anterior pterygoidal processes the pterygoids do not meet each other in the median line anterior to the interpterygoidal vacuity.

Anterior to the interpterygoidal vacuity the vomer lies in the median line and supports the anterior end of the parasphenoidal rostrum.

Further anteriorly lie the palatal sheets of the premaxilla forming a secondary palate.

The Therocephalia

In the Pristerognathidae the occiput is inclined forwards at an angle of 80° to the cranial base.

The long parasphenoidal rostrum is inclined upwards at an angle of 30°. Its anterior end lies free, unsupported by the pterygoid.

The exoccipital forms a small part of the posterior part of the brainfloor.

The sidewall of the braincase is widely open since the sphenoidal complex is usually not ossified.

The proötic is weakly developed, but forms a notch for the Vth nerve. The pair just meet in the middle line to form the upper part of the *dorsum sellae* with the basisphenoid lying lower down and also forming the floor of the *sella turcica*, which is very shallow.

The sphenoidal complex is only present in a specimen sectioned by Broom where it is feebly ossified.

In the median line the parasphenoidal rostrum is visible through the narrow interpterygoidal vacuity. Anteriorly the long anterior pterygoidal processes meet in the median line and carry only a low median septum.

Further anteriorly the long vomers lie in a nearly horizontal plane and form no dorsal septum.

The Gorgonopsia

Not having a gorgonopsian from the *Tapinocephalus* zone that could be sectioned I have to rely on a single specimen of a hipposaurid in which parts of the structures under consideration are visible.

The occiput is about at right angles to the cranial base.

The short parasphenoidal rostrum is inclined upwards at an angle of about 50° to the cranial base.

The exoccipital does not form part of the brainfloor.

The sidewall of the braincase is widely open between the otic and sphenoidal regions.

The proötic is weakly developed and apparently would not enclose the foramen for the Vth nerve.

The sphenoidal complex appears to be well developed with apparently a septal part formed by a septosphenoid and dorsal wings composed of the orbitosphenoids.

The interpterygoid vacuity is reduced and the short anterior pterygoidal processes meeting in the middle line anterior to the vacuity forms a high dorsal septum supporting the parasphenoid. Further anteriorly the long vomers carry a well-developed dorsal septum.

Derivation of the therapsids

If all the therapsids of the *Tapinocephalus* zone developed from a common ancestral group then that group must have been more primitive than the sphenacodont pelycosaurs (e.g. *Dimetrodon*).

Considering only the nature of the structures studied in this report it is clear that the ancestral group would have to be without the following characters developed by *Dimetrodon*:

1. The occiput would not be sloping forwards.
2. The proötic would not be present in the *dorsum sellae*.
3. The exoccipital would not form the posterior part of the brainfloor and the basioccipital would not be excluded from the brainfloor.

4. There would be no strongly developed dorsal median septa on the pterygoid or vomer.
5. The face would not be so downturned.

Even the ophiacodonts appear to be too advanced as far as the characters we are here considering are concerned.

Dinocephalia

If, however, the four therapsid groups of the *Tapinocephalus* zone arose from different groups of the pelycosaurs one could reasonably derive the Dinocephalia from a group very near to *Dimetrodon*. The developments shown by the Dinocephalia are: a backward sloping of the occiput for mechanical reasons associated with a changed function of the nuchal muscles and with a concomitant posterior shift of the braincase and greater strength in the sidewall of the braincase and an abnormal development of both the parietal organ and hypophyseal mass. The latter is related to the pathological pachyostosis which caused the extinction of the Dinocephalia before the end of *Tapinocephalus* zone times.

Dicynodontia

The morphological gap between the Dicynodontia of the *Tapinocephalus* zone and the Pelycosauria is so great that no known pelycosaur group can be envisaged as being directly ancestral. Even the Russian *Otsheria*, of which the relevant structures are mostly undetermined, does not provide pointers to an ancestral pelycosaur.

A forerunner of the Dicynodontia would have to be a form in which the proötic does not enter the *dorsum sellae*, the exoccipital is excluded from the brainfloor, no or weak dorsal pterygoidal septum, intermediately situated sphenoid complex and with the premaxilla just commencing to push the vomer posteriorly.

Such a form could not also be an ancestor of the Dinocephalia and Theriodontia.

Many other features of the dicynodont skeleton also point to a separate origin for these remarkable reptiles, which in their further development right up to *Kannemeyeria* in the Trias maintain their basically unique structure.

Therocephalia

The early pristerognathid Therocephalia are, in the features under discussion, more primitive than the sphenacodont pelycosaurs. The proötic is just entering the *dorsum sellae*, the exoccipital is just entering the posterior brainfloor, the anterior pterygoidal processes and vomers, although long, have as yet not developed dorsal median septa and lie horizontally in a plane just ventral to the cranial base and the sphenoidal complex has just started to ossify.

It would thus appear that the pristerognathids have advanced from a common ancestor with the sphenacodonts and ophiacodonts at a tempo of development somewhat less than the higher pelycosaurs.

This slower tempo in development makes the pristerognathids a group well suited for further advances in the direction of the mammals, which their descendants have in fact realized.

Gorgonopsia

Although the features under discussion are inadequately known in the Gorgonopsia of the *Tapinocephalus* zone it would appear that in them the tempo of development was rapid and the morphological stages reached further than that reached by the pelycosaurs. Knowledge of these structures in the Russian phthinosuchids may very well help to bridge the gap between Gorgonopsia and Pelycosauria.

In contrast to the Therocephalia the Gorgonopsia with their more rapid tempo achieved a higher stage of development quicker but their descendants thus committed were off the line leading to the mammals.

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